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UNTERSUCHUNGEN ÜBER DIE KONKURRENZWIRKUNG VON GEHÖLZWURZELN AUF ACKERKULTUREN

DER EINFLUSS VON EICHEN ALS STANDBÄUME IN HECKEN

von LORE STEUBING *)

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With English summary

I. EINLEITUNG

In den letzten Jahren hat die Anpflanzung von Hecken als Windschutz eine starke Förderung erfahren. Es mehren sich jedoch die Stimmen, die vor einer zu raschen Verallgemeinerung und Propagierung warnen, bevor nicht nur die mikroklimatische Bedeutung, sondern auch die zahlreichen anderen Probleme einer Heckenlandschaft geklärt sind (H a r t k e [2]). Hierher gehören vor allem die wirtschaftliche, bodenkundliche, betriebstechnische und die landschaftsökologische Seite, die noch einer vertieften Bearbeitung bedürfen. Ebenso wurde bisher die Frage, welchen Einfluß Gehölzwurzeln auf die anliegenden Feldkulturen ausüben, garnicht oder wenig beachtet. Bei der Auswahl der Pflanzen für eine Windschutzanlage wird fast nur berücksichtigt, welchen Nutzen die oberirdischen Teile bringen; um die "unterirdische Botanik", d.h. die Ausbreitung der Gehölzwurzeln im Acker kümmert man sich kaum. Angepflanzt werden bevorzugt Lieferanten von Wildobst oder solche Bäume und Sträucher, die sehr raschwüchsig sind und daher als Brennholz Verwendung finden oder aber gutes Nutzholz bringen (H i l f [3], S c h e e r e r [10], S c h m i d t [11], S e i f e r t [12]). Solche Nutzhölzer sind als Standbäume in den Hecken verbreitet. Hier trifft man Linde, Birke, Ahorn, Eiche und Pappel an, wobei

*) Der technischen Assistentin, Fräulein E d i t h a B ö h m e, sei für ihre tätige Mithilfe herzlich gedankt.

**) Direktor: Prof. Dr. M ü l l e r–S t o l l.

letzterer ein besonderes Interesse geschenkt wird. Mit dem Heranwachsen macht sich der mehr oder minder große Einfluß dieser Standbäume auf die angebauten Kulturen in zunehmendem Maße geltend. Verschiedentlich wird bereits darauf hingewiesen, daß sich unmittelbar am Rande einer Windschutzanlage eine Depression im Ernteertrag des Ackerlandes zeigt, wofür sowohl die Schattenspendung des Hindernisses als auch die Baumwurzeln verantwortlich seien (Kreutz [5]), Steubing [13]), Wendt [17])). Da bisher wenig experimentelle Beweise dieser Ansicht geliefert wurden, soll in vorliegender Arbeit, gestützt auf eigene Untersuchungen, den Ursachen für das schlechtere Wachstum der am Gehölzrand stockenden Kulturen nachgegangen werden. Im Einflußbereich von Eichen verringert sich die Vitalität vieler Pflanzen recht auffällig. So wurde zunächst die Bedeutung dieses Standbaumes für die Feldkulturen zu klären versucht.

II. VERSUCHSANORDNUNG

An der Nordseite unseres Versuchsgeländes zieht sich — durch eine schmale 0,50 m hohe Böschung getrennt — eine Ost-West gerichtete Allee entlang, die von etwa 60-jährigen Roteichen (*Quercus rubra*) bewachsen ist. Die Bäume stehen durchschnittlich in 8 m Abstand voneinander. Auf dem angrenzenden Kulturland wurden in Nord-Süd-Richtung 4 m breite und 28 m lange Feldstreifen als Versuchsflächen angelegt, auf denen Kartoffeln (Industrie), Runkeln (Eggendorfer Gelbe), Mohn (*Papaver somniferum oleiferum fl. albo*), Mais (Badischer Landmais) und Hafer (Siegeshafer) zum Anbau gelangten. Jeweils lagen 2 Streifen mit gleicher Bepflanzung nebeneinander. Der eine blieb ungedüngt, während der andere vor der Aussaat Gaben an Kalkammonsalpeter und Superphosphat erhielt, die 1,0 dz/ha bzw. 1,5 dz/ha entsprachen. Unmittelbar vor den mit Mais und Mohn besäten Feldstreifen wurde ein 15 m langer, 1,0 m tiefer und 0,50 m breiter Graben in 2 m Abstand von den Alleebäumen ausgehoben, bei seiner Ausschachtung wurden die Eichenwurzeln durchschnitten. Auf diese Weise war nicht nur ein Vergleich zwischen der nahe und entfernt von den Eichen stockenden Kulturen möglich, sondern auch zwischen Pflanzen, die einer Konkurrenz mit den Gehölzwurzeln ausgesetzt waren und solchen, bei denen die aktive Einwirkung der Baumwurzeln ausgeschaltet wurde.

In jedem Feldstreifen fand mit zunehmendem Abstand von den Bäumen eine Aufteilung in Parzellen von 2 m Seitenlänge und 4 m Breite statt. Alle Felder, einschließlich derer, vor denen der Graben entlang lief, begannen in 2 m Entfernung von den Eichen. Die Parzelle 1 lag demnach in 2–4 m, Parzelle 10 in 22–24 m Abstand. Das Pflanzenwachstum wurde laufend verfolgt und später der Ernteertrag der einzelnen Parzellen er-

mittelt. Um vorkommende Unterschiede im Mikroklima zwischen den Parzellen 1–10 zu erfassen, waren sowohl im Maisbestand als auch auf dem 0,50 m breiten Weg zwischen den Rübenfeldern in 0,50 m Höhe Meßstationen eingerichtet worden zur Erfassung der Niederschlagsmenge (Hellmannscher Regenmesser), des Taufalls (Leicksche Tauplatte), der Luftfeuchtigkeit und Temperatur (Aspirations-Psychrometer). Das Piche-Evaporimeter gab die Evaporation in 3 cm Höhe über dem Erdboden an. Außerdem wurden die Bodentemperaturen in 0 cm, 10 cm und 20 cm Tiefe gemessen. Die Bodenwassergehaltsbestimmung erfolgte durch Entnahme von Bohrproben aus einer mittleren Tiefe von 20 cm und anschließendes Trocknen bei 105°C. Nach Beendigung der Vegetationsperiode wurde durch Aufgraben die Reichweite und Tiefe der Eichenwurzeln im Ackerland festgestellt (Clements, Weaver and Hanson[1]).

III. MIKROKLIMATISCHE UNTERSUCHUNGEN

Das Mikroklima vermag die Entwicklung der Pflanzen weitgehend zu beeinflussen, da es sowohl in den Wärme- als auch in den Wasserhaushalt eingreift. Daher sind Temperatur und Feuchtigkeit die wichtigsten bioklimatischen Faktoren, deren Analyse erforderlich war. Eine Untersuchung der Lichtverhältnisse entfiel, weil eine Schattenwirkung der Eichen auf die angebauten Kulturen infolge der Nordstellung am Feldrand nicht auftreten konnte. Obwohl Temperatur und Feuchtigkeit eng miteinander verknüpft sind, sei ihre Besprechung getrennt vorgenommen.

1. *Temperatur*

Die Lufttemperatur wies nur an Strahlungstagen mit geringer Luftbewegung Unterschiede in den Parzellen 1–10 auf. Bei solcher Witterung lagen Maxima und Minima an der Meßstelle der Parzelle 1 höher als in den übrigen. Sobald am Morgen die Sonnenstrahlen das Versuchsfeld erreicht hatten, stieg die Temperatur in Parzelle 1 schneller an als in Parzelle 10 und erreichte auch einen höheren Mittagswert (Tabelle I).

TABELLE I

Lufttemperatur in 0,50 m Höhe in den Parzellen 1 und 10

Datum	Uhrzeit	Temperatur in °C		
		Parzelle Nr. 1	Parzelle Nr. 10	Differenz
16.VII. 1953	8°°	22,2	21,5	0,7
	10	25,6	24,5	1,1
	12	30,3	27,8	2,5
	14	27,4	24,6	2,8
	17	17,2	16,6	0,6

Dieser ergab sich durch eine — wenn auch geringfügige — Luftstauung am Rande der Straßenböschung. In Parzelle 10 war dagegen die Behinderung des Luftmassenaustausches geringer und daher auch die Temperatur niedriger. Die schnellere Erwärmung der baumnahen Parzellen beruhte in Schönwetterperioden wohl mit auf der stark verminderten Taubildung in diesem Bereich. Während hier der trockene Boden bereits aufgeheizt wurde und seine Wärme an die Luft abgeben konnte, mußte in weiterem Abstand von den Eichen die eingestrahlte Sonnenenergie zunächst zur Verdunstung des Boden und Pflanzen reichlich benetzenden Taus verbraucht werden. Nachts sank die Temperatur unter den Bäumen weniger als in größerer Entfernung ab, weil die Ausstrahlung durch die Gegenstrahlung der Baumkronen gehemmt war (Fig. 1).

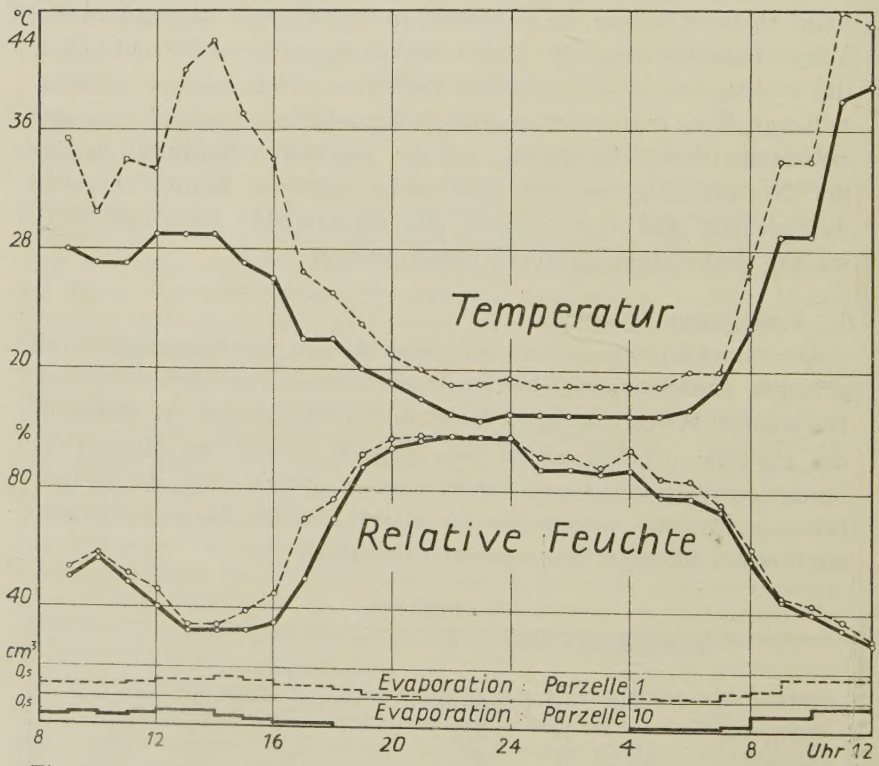

Fig. 1. Verlauf von Temperatur (in °C), relativer Feuchtigkeit (in %) und Evaporation (in cm^3) in Parzelle 1 (gestrichelte Linie) und 10 (ausgezogene Linie).

Die differierenden Wärmegrade in den Parzellen 1 und 10 wurden noch deutlicher, wenn statt der Luft- die Bodentemperatur gemessen wurde. Die größten Unterschiede zwischen den beiden Parzellen ergaben sich bei Messungen unmittelbar an der Erdoberfläche. In den tieferen Bodenhorizonten schwanden die Differenzen. Aus Tabelle II geht hervor, daß die höchsten Temperaturen wiederum unter den Bäumen gemessen wurden. Auch war hier die Schwankungsbreite der Extremwerte am größten.

TABELLE II

Temperatur (°C) an der Erdoberfläche in Parzelle 1 und 10 über vegetationslosem Boden und im Maisbestand

Datum	Zeit	Vegetationsloser Boden (Weg)			Maisbestand		
		Parzelle Nr.		Differenz	Parzelle Nr.		Differenz
		1	10		1	10	
	6°°	20,0	20,0	0,0	18,1	17,2	0,9
	9	35,4	25,5	9,9	28,8	23,4	5,4
	12	36,1	30,7	5,8	29,2	18,6	10,6
21./22.	15	36,0	34,0	2,0	31,1	28,6	2,5
VII.1953	18	26,1	29,3	—3,2	23,0	25,3	—2,3
	21	20,7	19,5	—1,2	19,4	17,1	—2,3
	24	19,2	18,9	—0,3	17,5	16,9	0,6
	3	19,1	18,9	0,2	17,4	16,9	0,5
	6	20,1	20,0	0,1	18,0	17,6	0,4
Schwankungsbreite		17,0	15,1		13,7	11,7	

Ferner zeigt ein Vergleich der auf dem unbewachsenen Weg ermittelten Werte mit denen des Maisbestandes, daß der stärkere Schluß der Pflanzen zu einer Behinderung der Ein- und Ausstrahlung führte, und daher die Differenzen zwischen Parzelle 1 und 10 geringer als auf dem vegetationslosen Boden waren.

2. *Feuchtigkeit*

Die unterschiedlichen Feuchtigkeitsverhältnisse in den einzelnen Parzellen spiegeln sich am besten in der Niederschlagshöhe wieder. Allerdings übten hierbei Windstärke und die Richtung, aus der der Regen kam, einen maßgeblichen Einfluß auf die vom Meßgerät eingefangene Wassermenge aus. So wurde bei südlichen Winden der mitgeführte Niederschlag wesentlich weiter in die baumnahen Parzellen hineingedrückt, als bei den aus N oder NW kommenden Niederschlägen. Die Baumkronen selbst wirkten wie ein mächtiger Schirm, der leichte Regen abfing und erst bei stärke-

ren Güssen das nicht von Ästen und Stamm abgeleitete Wasser durchließ. Fielen die Niederschläge schräg aus nord-westlicher Richtung ein, so vergrößerte sich die Regenschattenzone über die dicht an den Baumstämmen gelegenen Parzellen hinaus. Aus der in Fig. 2 dargestellten Messung vom 26./27.VI.1953 wird der Anstieg der Niederschlagshöhe mit zunehmendem Abstand von den Bäumen deutlich. Parzelle 10 erhielt doppelt so viel Regen wie Parzelle 1. Während die Differenz in der Niederschlagshöhe von Parzelle 1 zu Parzelle 2 nur 0,6 mm betrug, vergrößerte sie sich bereits in Parzelle 3 auf 1,6 mm und lag in 5 sogar schon 3,4 mm höher.

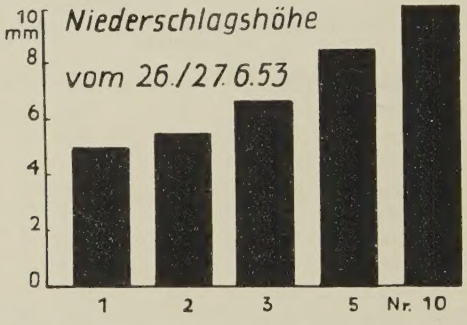

Fig. 2. Niederschlagshöhe (in mm) in den Parzellen 1, 2, 3, 5 und 10 am 26./27.VI.53.

Die mit zunehmendem Abstand von den Eichen verbesserte Feuchtigkeitsspendung trat natürlich nur bei den von N oder NW über die Bäume streichenden Winden und den von ihnen mitgeführten Niederschlägen auf. Bei Einbeziehung des aus anderen Richtungen kommenden Regens änderte sich das angegebene Verteilungsschema, und es konnten u.U. sogar die höchsten Niederschlagsmengen in den baumnahen Parzellen gemessen werden. Die Monatsbilanz schloß aber trotzdem mit einem Wasserdefizit für die Parzellen im Bereich der Baumkronen ab. So wurden in der Zeit vom 26.VI.–26.VII.1953 8 Regentage verzeichnet, an denen in den Parzellen folgende Niederschlagsmengen gemessen wurden (Tabelle III). Es steigerte sich somit auch im Monatsmittel die Regenhöhe beim Übergang von Parzelle 1 zu Parzelle 10 um den fast doppelten Betrag.

TABELLE III

Niederschlag in den Parzellen 1–10 während der Zeit vom 26.VI.–26.VII.53		
Parzelle Nr.	Regen in mm	%
1	41,8	53,2
2	51,7	65,8
3	53,5	68,2
5	64,3	81,9
10	78,5	100,0

Die reichlichere Niederschlagsspendung mit zunehmender Entfernung von den Eichen kam nicht nur bei der Messung des geformten Niederschlages (Regen) zum Ausdruck, sondern auch im Taufall. Tabelle IV zeigt, daß in windstillen Nächten die günstigeren Ausstrahlungsbedingungen in den entfernteren Parzellen zu einer verstärkten atmosphärischen Berieselung führten.

TABELLE IV

Taufall in den Parzellen 1–10		
Datum	Parzelle Nr.	Taufall in g/dm²
8.IX.53	1	0,05
	2	0,06
	3	0,09
	4	0,15
	5	0,17
	6	0,19
	8	0,22
	10	0,20

Die erhöhte Regen- und Tauspendung machte sich ebenfalls in den Werten für die Luftfeuchtigkeit bemerkbar, die in Parzelle 10 über denen der Parzelle 1 lagen (Fig. 1). Daraus folgt aber auch, daß die ungünstigeren Feuchtigkeitsverhältnisse in den baumnahen Parzellen zu einer erhöhten Evaporation Veranlassung geben mußten. Mit zunehmendem Abstand von den Eichen verringerte sich der Verdunstungszwang (Tabelle V u. Fig. 1).

Auch die Bodenfeuchtigkeit war in der Einflußzone der Eichen geringer als außerhalb. Hier mußte allerdings die Frage geklärt werden, wie weit diese Verminderung auf einer Regenschattenwirkung der Baumkrone beruhte und wie weit auf einem Wasserentzug durch die Gehölzwurzeln. Daher wurden Bodenproben aus den Parzellen 1–10 sowohl aus einem Feldstreifen mit unbe-

TABELLE V

Evaporation in 3 cm Höhe über unbewachsenem Boden in den Parzellen 1 und 10 gemessen mit Piche-Evaporimeter, 3 cm Scheibe grün

Datum	Zeit	Evaporation in cm^3		
		Parzelle Nr. 1	Parzelle Nr. 10	Differenz 1–10
1.VII.53	8–9°°	0,60	0,50	0,10
	9–10	1,10	0,85	0,25
	10–11	0,95	0,70	0,25
	11–12	0,90	0,70	0,20
	12–13	0,85	0,70	0,15
	13–14	0,80	0,70	0,10
	14–15	0,60	0,60	0,00
	15–16	0,50	0,45	0,05

schädigten als aus dem entsprechenden mit durchschnittenen Eichenwurzeln gesammelt und der Wassergehalt bestimmt. Aus Fig. 3 geht hervor, daß sich das Abfangen des Regens durch das

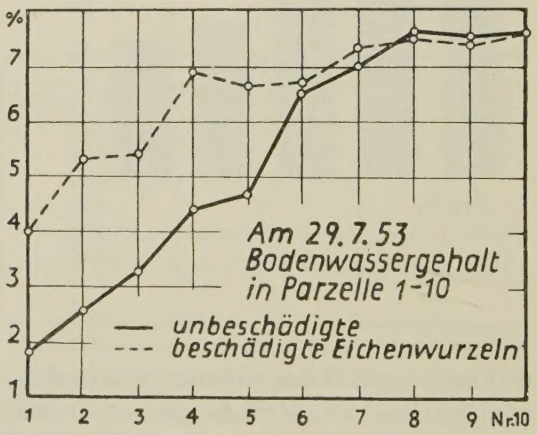

Fig. 3. Bodenwassergehalt (in Prozent des Frischgewichtes und mittlerer Tiefe von 20 cm) in den Parzellen 1–10. Messung im Acker mit durchschnittenen und nicht durchschnittenen Eichenwurzeln.

Blätterdach in einem Boden–Wasserdefizit in den baumnahen Parzellen deutlich ausprägte. Der Wassergehalt des Bodens war aber im Ackerland, vor dem der Graben entlanglief, an den ersten Meßstellen doppelt so hoch wie der des Vergleichsackers. Daher konnte diese Differenz nur durch den Wasserentzug der Gehölzwurzeln entstanden sein. Erst von Parzelle 6 an, d.h. in etwa 12 m Entfernung von den Eichen, traten keine größeren Abweichungen

zwischen den verglichenen Probestellen mehr auf. Bei den zu Abschluß des Versuches durchgeführten Grabungen ergab sich, daß die Hauptmasse der Eichenwurzeln in dieser Zone ihr Ende gefunden hatte.

IV. DIE BEEINFLUSSUNG DER VEGETATIONSENTWICKLUNG DURCH EICHEN

Die angebauten Kulturen (Mais, Mohn, Kartoffeln, Hafer, Rüben) wiesen mit zunehmender Entfernung von den Eichen besseres Wachstum und höhere Erträge auf. Die ungünstigeren Lebensbedingungen in den baumnahen Parzellen machten sich bereits beim Auflaufen der Saat von Mohn und Rüben bemerkbar. Infolge einer anschließenden Trockenperiode kamen — vorwiegend im Einflußbereich der Bäume — nur wenig Pflanzen hoch. In den Rübenparzellen traten in dieser Zone ausgedehnte Fehlstellen auf, Mohn mußte völlig neu eingesät werden. Das besonders schlechte Auflaufen des Mohns war nicht allein auf die ungünstige Wasserbilanz in Baumnähe zurückzuführen, denn Eichenlaub wirkt auf Mohnsamen stark keimungshemmend und -verzögernd (Winter u. Willeke[19]). Die heranwachsenden Versuchspflanzen wurden in bestimmten Zeitabständen bonitiert. In Schönwetterperioden war das starke Anwelken der Rübenblätter in den baumnahen Parzellen besonders auffällig (Steubing[13]), Taf. I). Ähnliche Dürreschäden ließen sich bei Kartoffeln beobachten. (Taf. II). Hier fiel nicht nur das Erschlaffen und der Kümmerwuchs der in den baumnahen Parzellen wachsenden Pflanzen auf, sondern auch der geringere und zugleich etwas verzögerte Blühansatz. Mais und Hafer blieben in ihrer Wuchshöhe im Einflußbereich der Eichen weit hinter den entfernter stehenden Pflanzen zurück. Wie sehr die Gesamtentwicklung von Hafer durch Konkurrenzwirkung beeinflusst wird, ergaben Versuche Pavlychenkos und Harringtons[9]). Einzeln stehende Haferpflanzen wiesen ein 10 fach besseres Spross- und Wurzelsystem auf als solche Pflanzen, die dicht nebeneinander in Drillsaat wuchsen. Der Mais zeigte außerdem in den ersten 3 Parzellen starke Chlorose. Auf den gedüngten Feldstreifen standen die angebauten Kulturen besser, aber Wachstums- und Ertragsunterschiede zwischen den baumnahe und entfernt stockenden Pflanzen waren ebenfalls vorhanden (Tabellen VI u. VII).

TABELLE VI

Durchschnittsgröße verschiedener Kulturen auf gedüngtem und ungedüngten Boden in Parzelle 1 und 10

Datum	Kultur	Ungedüngt			Gedüngt		
		Höhe in cm		Differenz	Höhe in cm		Differenz
		Parz. 1	Parz. 10	in cm	Parz. 1	Parz. 10	in cm
11.VII	Rüben	23,4	27,3	3,9	26,3	31,9	5,6
11.VII	Hafer	85,3	105,8	20,5	89,2	107,1	17,9
8.VII	Kartoffeln . .	43,0	60,0	17,0	50,4	58,0	7,6
30.VII	Mais	97,0	199,8	102,8	119,5	196,0	76,5

TABELLE VII

Ernteertrag verschiedener Kulturen auf gedüngtem und ungedüngten Boden in Parzelle 1 und 10

Datum	Kultur	Ungedüngt			Gedüngt		
		Ertrag in kg		Differenz	Ertrag in kg		Differenz
		Parz. 1	Parz. 10	in kg	Parz. 1	Parz. 10	in kg
9.X	Rüben	0,080	4,720	4,640	0,220	14,350	14,130
	Hafer	0,200	0,550	0,350	0,250	0,790	0,540
30.IX	Kartoffeln . .	1,020	14,470	13,450	0,920	9,800	8,880
	Mais	0,015	3,495	3,480	0.075	3,620	3,545

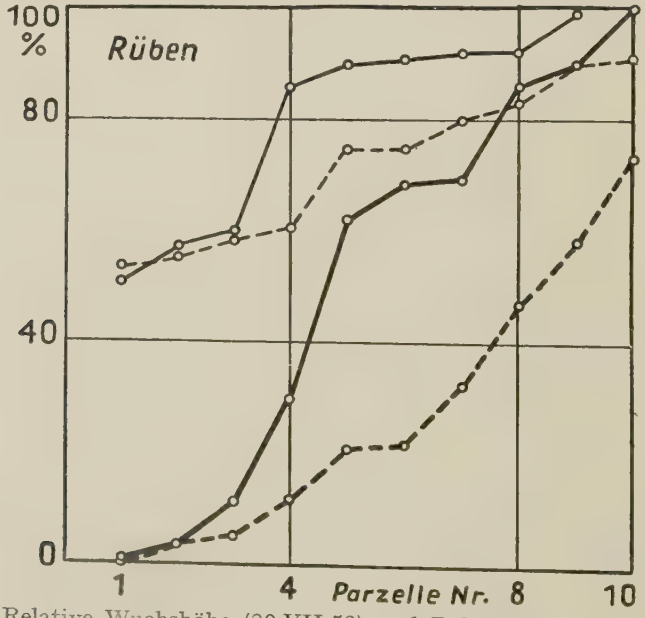

Fig. 4. Relative Wuchshöhe (30.VII.53) und Relativ-Ertrag von Rüben. (*Dünne Kurven*: rel. Wuchshöhe; *kräftige Kurven*: rel. Ertrag; *ausgezogene Linien:* gedüngt; *gestrichelte Linien*: ungedüngt. Höchstertrag im gedüngten Feldstreifen = 100).

In Fig. 4 sind die relative Wuchshöhe und der Relativertrag des Rübenversuchs für die einzelnen Parzellen aufgeführt. (Der im gedüngten Feldstreifen erreichte Höchstwert wurde = 100 gesetzt.) Das Kurvenbild verdeutlicht, daß die Wuchshöhe im Bereich der Eichen eine weit geringere Depression als der Ernteertrag erfuhr. Während die durchschnittliche Höhe der Rüben in den ersten Parzellen um rund 50% erniedrigt war, wurde der Ertrag in dem gleichen Bereich um etwa 95% herabgesetzt. Bis zur dritten Parzelle hin liegen die Kurven für den gedüngten und ungedüngten Feldstreifen dicht zusammen, um dann aber stark zu divergieren. Das fortan bessere Gedeihen der Kulturen auf den gedüngten Feldstreifen führt zu der Schlußfolgerung, daß in den ersten 3 Parzellen dem Wasserfaktor die entscheidende Rolle zukam, während in den nachfolgenden die Bodendüngung immer mehr Geltung gewann.

TABELLE VIII

Ergebnis der Bonitierung in den von Baumwurzeln durchzogenen gedüngten und ungedüngten Feldstreifen. (Berechnung nach der Differenzmethode (M u d r a, [7])) *)

Datum	Mittlerer Ertrag pro Feld	Gedüngt	Ungedüngt	D	t	P%	Sicherung
	Hafer						
17.VI. 53	Wuchshöhe	72,4	75,9	3,5	1,34	22,6	
11.VII. 53	in cm	103,12	96,7	—6,42	—2,47	3,4	gesichert
9.X. 53	Ernte in kg:						
	Stroh u. Korn	5,5	4,4	—1,1	—4,07	0,29	gut gesichert
	Kartoffeln						
17.VI. 53	Wuchshöhe	27,28	26,52	—0,76	—0,45	70,0	
8.VII. 53	in cm	52,49	51,3	—1,64	—0,67	50,2	
19.VIII. 53		66,59	62,08	—4,51	—1,45	16,7	
30.IX. 53	Ernte in kg	6,52	5,89	—0,63	—1,7	12,4	
	Rüben						
11.VII. 53	Wuchshöhe	32,46	26,27	—6,19	—6,87	0,1	sehr gut ges.
30.VII. 53	in cm	41,60	36,77	—4,83	—2,44	4,0	gesichert
19.VIII. 53		40,96	35,61	—5,35	—2,43	4,0	gesichert
9.X. 53	Ernte in kg:						
	Wurzeln	23,11	12,21	—10,9	—3,2	1,08	gut gesichert
	Blätter	9,34	5,37	— 3,97	—3,7	0,5	gut gesichert

*) D = Differenz zweier Mittelwerte; $t = D/mD$ (mD = Fehler der Differenz)
P = Grenzwahrscheinlichkeit.

Überblickt man die in Tabelle VIII zusammengestellten Ergebnisse, so fällt auf, dass die statistische Sicherung einer besseren Wachstums- und Ertragshöhe durch Mineralstoffdüngung nicht

immer gegeben war. Bodenunterschiede in der Versuchsfläche, vor allem aber ein stellenweiser stärkerer Nährstoffentzug durch lokale Anhäufung von Baumwurzeln sind hierfür verantwortlich zu machen. Wie sehr der Bodenwassergehalt das Pflanzenwachstum beeinflußt, erwies sich besonders im Mohn–Anbauversuch. Trotz der zweimaligen Einsaat war in der baumnahen, von intakten Eichenwurzeln durchzogenen Zone der Bestand zu dürftig, als daß die vereinzelt stehenden Kümmerpflanzen zur Auswertung hätten

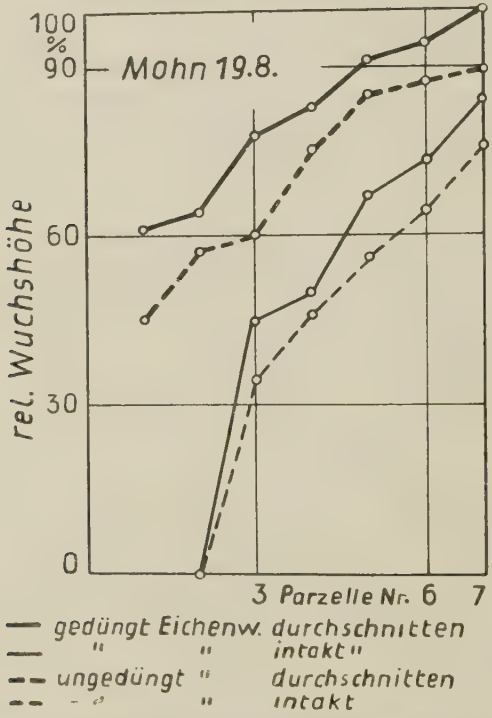

Fig. 5. Relative Wuchshöhe von Mohn auf gedüngtem und ungedüngten Ackerland, das von durchschnittenen bzw. nicht durchschnittenen Eichenwurzeln durchzogen wurde. (Höchstertrag im gedüngten Feldstreifen mit durchschnittenen Wurzeln = 100).

benutzt werden können (Taf. III). Führte dagegen vor dem Ackerland der Graben entlang, der die Baumwurzeln von der Mutterpflanze abtrennte, so lief wenigstens ein Teil der Mohnsaat auf. Hier konnten die Bonitierungen bereits von der ersten Parzelle an vorgenommen werden, während in den Feldstreifen, die von unbe-

schädigten Gehölzwurzeln durchzogen wurden, eine Auswertung erst von der dritten Parzelle an möglich war (Fig. 5). Aus der graphischen Darstellung geht hervor, daß der Mohn auf ein Durchschneiden der Baumwurzeln mit einer gesteigerten Wuchsfreudigkeit reagierte. Die vegetative Entwicklung wurde durch diese einfache kulturtechnische Maßnahme derartig gefördert, daß sogar im ungedüngten Feldstreifen der Pflanzenwuchs besser war als im gedüngten, jedoch von intakten Eichenwurzeln durchsetzten Ackerland (Tabelle IX). (Eine Bestimmung des Ernteertrages für Mohn mußte entfallen, da die Vögel die meisten Kapseln ausgefressen hatten.)

TABELLE IX

Durchschnittsgröße bei Mohn in Abhängigkeit von der Baumwurzelkonkurrenz

Datum	Parz.Nr.	Höhe in cm					
		Ungedüngt			Gedüngt		
		Baumwurzeln		Differenz	Baumwurzeln		Differenz
		mit	ohne		mit	ohne	
17.VI.53	1	—	37,2	37,2	—	52,5	52,5
	2	—	48,1	48,1	—	53,6	53,6
	3	28,0	50,1	22,1	38,2	65,7	27,5
	4	38,6	63,0	24,4	55,9	68,3	12,4
	5	47,4	70,8	23,4	60,9	76,3	15,4
	6	54,0	72,0	18,0	65,4	78,3	12,9
	7	63,6	74,0	10,4	69,6	83,5	13,9

Eine bessere Versuchsauswertung konnte bei Mais vorgenommen werden. Hier war auch in den baumnahen Parzellen die Saat gut aufgelaufen. Frühzeitig machten sich aber bei den Kulturen die unterschiedlichen Lebensbedingungen in den einzelnen Feldstreifen geltend. Bereits bei den Jungpflanzen fiel in Baumnähe die starke Chlorose auf; sie trat bei den ungedüngten Pflanzen weitaus mehr als bei den gedüngten in Erscheinung. Dieser Sachverhalt erfuhr eine merkliche Abschwächung in den Feldstreifen, vor denen der die Baumwurzeln abtrennende Graben entlanglief. Hier waren die ungedüngten Pflanzen nur noch leicht chlorotisch, die gedüngten zeigten normales Aussehen. Ebenso machte sich das bessere Wachstum dieser nicht mehr unter Baumwurzelkonkurrenz stehenden Pflanzen bei den Höhenmessungen bemerkbar (Tabelle X). Der Mais war in den "Graben-Parzellen" nicht nur höher, sondern es verringerten sich auch mehr als auf den Vergleichsflächen die

Größenunterschiede zwischen den baumnahe und entfernt stehenden Pflanzen (Tabelle XI).

TABELLE X

Durchschnittsgröße bei Mais in Abhängigkeit von der Baumwurzelkonkurrenz							
Datum	Parz. Nr.	Höhe in cm					
		Ungedüngt			Gedüngt		
		Baumwurzeln		Differenz	Baumwurzeln		Differenz
		mit	ohne	in cm	mit	ohne	in cm
11.VII. 1953	1	97,0	119,9	22,9	119,5	183,2	63,7
	2	108,4	162,0	53,6	132,1	186,8	54,7
	3	125,8	154.1	28,3	147,3	187,0	39,7
	4	153,2	169,9	16,7	164,6	179,2	14,6
	5	169,5	185,3	15,8	179,6	188,4	8,8
	6	186,3	188,3	2,0	163,1	209,1	46,0
	7	190,4	187,8	—2,6	192,3	200,1	7,8
	8	187,3	203,7	16,4	202,4	199,4	—3,0
	9	199,8	200,0	0,2	195,8	194,2	—1,6
	10	212,3	205,3	—7,0	196,2	207,2	11,0

TABELLE XI

Größenunterschied bei Mais zwischen der schlechtesten und der besten Parzelle im Feldstreifen				
Datum	Schwankungsbreite der Extremwerte in cm			
	Ungedüngt		Gedüngt	
	Baumwurzeln		Baumwurzeln	
	mit	ohne	mit	ohne
17.VI. 53	20,6	18,0	14,5	14,0
20.VII.53	115,3	85,4	82,9	24,0

Aus den Angaben der Tabelle XI geht hervor, daß sich die Eichenwurzelkonkurrenz mit fortschreitender Vegetationsentwicklung immer deutlicher auswirkte. Je höher der Wasser- und Nährstoffbedarf der erstarkenden Maispflanzen wurde, desto ungünstiger mußte sich ein Entzug durch die Gehölzwurzeln auswirken. Da der Boden vor der Bestellung gedüngt worden war, so gelangten die zugefügten Mineralstoffe mit dem Regenwasser nach und nach in das Erdreich und konnten von den Maiswurzeln abgefangen werden. Daher war der Wuchsunterschied zwischen den Pflanzen in Baumnähe und den weiter entfernt und daher besser stehenden hier auch nicht so gross wie auf den ungedüngten Feldern. Auf letzteren trat die Konkurrenz um die im Boden vorhandenen Nährstoffe weitaus

mehr als im gedüngten Ackerland in Erscheinung, wo die entscheidende Bedeutung dem Wasserentzug durch die Baumwurzeln zufiel. Aus den Figuren 6 und 7 geht hervor, daß sich auch bei Mais die relative Wuchshöhe im Einflußbereich der Eichen viel weniger verringerte als der Ernteertrag. In der gedüngten, von intakten Gehölzwurzeln durchzogenen Parzelle 1 wurde die Größe der Pflanzen um 40 %, bei Ausschaltung der Eichenwurzelkonkurrenz um nur 15 % gesenkt, bezüglich des Ertrags fand dagegen in den gleichen Teilstücken eine Depression um 97 % bzw. 70 % statt. Die ungedüngte Parzelle 1 brachte bei intakten Eichenwurzeln eine Verminderung der Wuchshöhe um 55 %, die beim Durchschneiden der Wurzeln auf 45 % absank, für den Relativertrag betrugen die entsprechenden Werte 99 % bzw. 97 %.

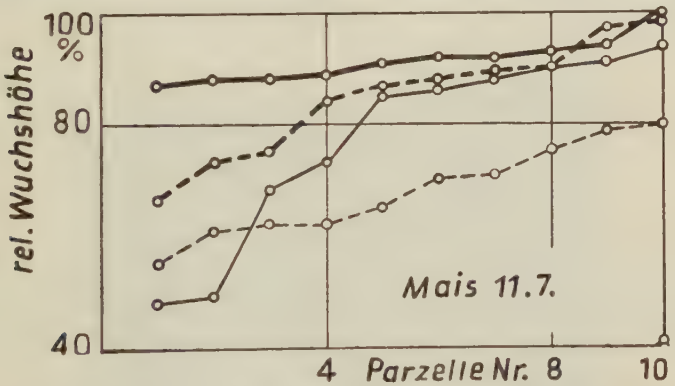

Fig. 6. Relative Wuchshöhe von Mais auf gedüngtem und ungedüngten Ackerland, das von durchschnittenen bzw. nicht durchschnittenen Eichenwurzeln durchzogen wurde. (Höchstertrag im gedüngten Feldstreifen mit durchschnittenen Wurzeln = 100).

In Tabelle XII sind die Ergebnisse verschiedener Bonitierungen an Mais aufgeführt. In den von aktiven Baumwurzeln durchzogenen Versuchsflächen liegen — auch bei Bestimmung des Durchschnittsertrags für den gesamten Feldstreifen — die Werte fast ausnahmslos unter denen der "Graben-Parzellen". Vergleicht man den Ertrag der ungedüngten mit den gedüngten Parzellen, so ist eine statistische Sicherung in den Feldern mit durchschnittenen Wurzeln eher als in den Versuchsflächen gegeben, in denen eine Ausschaltung der Baumwurzeln nicht vorgenommen worden war.

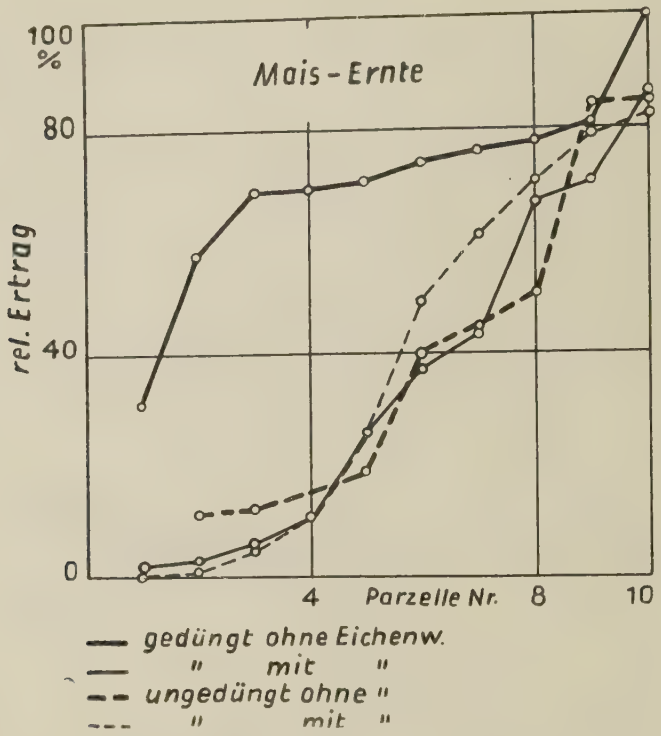

Fig. 7. Relativ-Ertrag von Mais auf gedüngtem und ungedüngten Ackerland, das von durchschnittenen und nicht durchschnittenen Eichenwurzeln durchzogen wurde. (Höchstertrag im gedüngten Feldstreifen mit durchschnittenen Wurzeln = 100).

TABELLE XII

Bonitierungen bei Mais in Abhängigkeit von der Baumwurzelkonkurrenz

Datum	Mittlerer Ertrag pro Parzelle	± Baumwurzeln	Gedüngt	Ungedüngt	*D*	*t*	*P*%	Sicherung
7.VI.53	Wuchshöhe	mit	56,47	56,08	— 0,39	—0,36	70,0	
	in cm	ohne	60,98	56,77	— 4,21	—1,91	7,7	
30.VII.53	Wuchshöhe	mit	169,35	163,00	— 6,35	—1,20	25,9	
	in cm	ohne	193,55	177,65	—15,90	—2,28	4,8	gesichert
30.IX.53	Ernte in kg	mit	1,485	1,635	+ 0,15	1,5	16,7	
		ohne	2,975	1,625	— 1,34	—5,56	kl.0,1	sehr gut gesichert

Der Einfluß der Eichen machte sich nicht nur bei den angebauten Kulturen geltend, sondern erstreckte sich auch auf die Unkrautflora. Betrachtet man die für die einzelnen Parzellen aufgestellte Pflanzenliste (Tabelle XIII), so fällt sofort auf, daß die baumnahen Abschnitte arten-

Taf. 1: Dürreschäden an Rüben in den baumnahen Parzellen.

Taf. 2: Dürreschäden an Kartoffeln in den baumnahen Parzellen. Im Hintergrund blühende Kartoffeln.

Taf. 3: Verringerung der Wuchsfreudigkeit und Fehlstellen bei Mohn mit Annäherung an die Eichen.

Taf. 4: Verlauf zweier Eichenwurzeln im Acker. Der Deutlichkeit halber wurden die Wurzeln gekalkt.

ärmer als die weiter entfernt liegenden sind. Während für Parzelle 1 nur fünf Arten eingetragen sind, hat sich in Parzelle 10 die Zahl der Pflanzenarten auf 17 erhöht.

TABELLE XIII

Deckungsgrad und Soziabilität von Ackerunkräutern mit zunehmender Entfernung von den Eichen (26.VII.53) nach den in der Pflanzensoziologie üblichen Skalenwerten

Pflanzenart	Parzelle Nr.									
	1	2	3	4	5	6	7	8	9	10
Panicum lineare	4.5	4.5	4.5	4.4	3.4	2.3	4.4	2.3	2.3	2.3
Chenopodium album	3.4	3.2	3.4	3.4	4.4	4.4	4.4	4.5	4.5	3.4
Equisetum arvense	2.3	2.2	2.2	3.4	4.4	3.4	2.3	2.3	1.2	1.2
Rumex acetosella	2.2	2.2	2.3	2.2	3.4	3.4	1.2	1.2	+.1	+.1
Oxalis stricta	1.1	—	3.3	2.3	3.4	2.3	3.3	1.2	1.2	—
Melandrium album	—	—	1.1	1.1	1.2	1.2	+.1	1.2	1.2	+.1
Veronica arvensis	—	—	+.1	—	+.1	—	—	+.1	1.2	1.2
Panicum sanguinale	—	—	2.2	2.2	+.1	—	—	—	—	—
Galinsoga parviflora	—	—	—	2.2	2.3	4.4	3.4	3.4	3.4	4.5
Stellaria media	—	—	—	1.2	+.1	3.4	3.4	3.4	2.3	1.2
Capsella bursa pastoris	—	—	—	1.1	1.2	2.3	1.2	+.1	1.2	+.1
Geranium pusillum	—	—	—	+.1	+.1	2.3	1.2	1.2	2.3	2.3
Senecio vulgaris	—	—	—	1.2	+.1	1.2	1.2	+.1	+.1	+.1
Sonchus asper	—	—	—	+.1	+.1	1.2	1.2	+.1	+.1	+.1
Myosotis arenaria	—	—	—	+.1	—	+.1	—	—	+.1	—
Fumaria officinalis	—	—	—	—	1.2	—	—	1.1	—	1.1
Erigeron canadensis	—	—	—	—	+.1	+.1	—	—	+.1	—
Anagallis arvensis	—	—	—	—	—	+.1	+.1	—	—	—
Erysimum cheiranthoides	—	—	—	—	—	—	+.1	+.1	+.1	+.1
Rubus spec.	—	—	—	—	—	—	—	1.2	1.1	—
Leontodon hispidus	—	—	—	—	—	—	—	1.2	—	—
Daucus carota	—	—	—	—	—	—	—	—	3.4	4.4
Convolvulus arvensis										
Polygonum convolvulus	—	—	—	—	—	—	—	—	—	1.1
Vicia hirsuta	—	—	—	—	—	—	—	—	—	+.1

Neben der Zusammensetzung veränderte sich mit zunehmender Entfernung von den Bäumen auch die Größe der Unkräuter. Je mehr die Pflanzen aus dem Wirkungsbereich der Eichen herausrückten, desto besser wurde ihre Vitalität, die sich in einer erhöhten Wuchsfreudigkeit, Blüh- und Samenansatz äußerte (Tabelle XIV).

TABELLE XIV

Durchschnittsgröße von Ackerunkräutern mit zunehmender Entfernung von den Eichen (26.VII.53)

Pflanzenart	Höhe in cm in Parzelle Nr.:							
	1	2	3	4	5	6	7	8
Chenopodium album	20,0	17,1	22,0	31,3	39,1	40,0	39,9	42,0
Equisetum arvense	15,0	26,9	22,1	23,5	27,0	24,9	29,6	23,4
Panicum lineare	20,0	19,0	25,5	25,6	33,2	29,0	38,1	34,2
Galinsoga parviflora	—	—	—	17,2	32,0	39,0	39,4	43,7

V. WURZELGRABUNGEN

Nach dem Abernten der Kulturen konnten auf den leergeräumten Feldern Grabungen vorgenommen werden, um den Baumwurzelverlauf zu untersuchen. Mit zunehmendem Abstand wurden zur Eichenallee parallel verlaufende Gräben von 5 m Länge, 0,50 m Breite und 1,0 m Tiefe ausgehoben; anschließend wurden die im Bodenprofil vorhandenen Wurzeln ausgezählt, ihr Durchmesser ermittelt und das Ergebnis zeichnerisch festgehalten (Fig. 8). Nur mit dieser Methode ließen sich auch die feineren Wurzeln im Acker erfassen und deren Reichweite bestimmen. Außerdem wurde an anderen Stellen dem Verlauf der Wurzeln mit dem Spaten nachgegangen.

Der Boden wies eine schwärzlich grau gefärbte Ackerkrume von etwa 0,25 m Mächtigkeit auf. Es schloß sich ein bis 1,05 m Tiefe reichender B_1-Horizont aus anlehmigem Sand an, auf den ein B_2-Horizont aus sandigem Lehm folgte. Die Hauptmasse der Eichenwurzeln fand sich in 0,30–0,60 m Tiefe, nur einige wenige drangen bis zu 1,0 m hinab. Dicht am Baumstamm waren — wie aus dem Bodenprofil des in Fig. 8 (I) dargestellten ersten Grabens hervorgeht — allerdings auch in den oberen Bodenschichten zahlreiche schwächere Wurzeln vorhanden. Sie reichten aber nur bis zu der Zone, an der alljährlich der Umbruch des Bodens durch die Pflugschar begann. Eine größere Anzahl dieser flach streichenden Wurzeln konnte die Reichweite im Acker dadurch verlängern, daß sie mit dem Eintritt in das bebaute Land schräg abwärts in tiefer liegende Erdschichten eindrangen, von denen sie häufig wieder in bogenförmigem Verlauf bis zur Pflugsohlengrenze aufstiegen. In Stammnähe waren Anzahl und Dichte der Wurzeln am höchsten. So konnten in dem ersten Graben, der in $1\frac{1}{2}$ m Entfernung von den Eichen angelegt worden war, 327 Wurzeln auf der 5 m² breiten senkrechten Bodenfläche gezählt werden. Im zweiten, 4 m entfernten Graben waren noch 238 Wurzeln vorhanden, im dritten Graben (7 m Abstand) 153, im vierten (10 m Abstand) 119 und im fünften (12 m Abstand) noch 14 Wurzeln. Die maximale Reichweite im Acker betrug 16 m. Auch die freigelegten Wurzeln anderer Eichenbäume besaßen eine etwa gleich große horizontale wie vertikale Ausdehnung. Bei diesen Grabungen fiel die in unmittelbarer Nähe der Stammbasis einsetzende reiche Verästelung der Wurzeln auf

(Tafel IV). Die Aufspaltung der kräftigen Haupt- in zahlreiche dünnere Seitenwurzeln erklärte auch die rasche Abnahme des Wurzeldurchmessers beim Übergang vom 1. zum 2. und 3. Graben. Die Verästelung nahm zu den Enden hin merklich ab. Der Verlauf der Wurzeln war sowohl in waagerechter wie in senkrechter Rich-

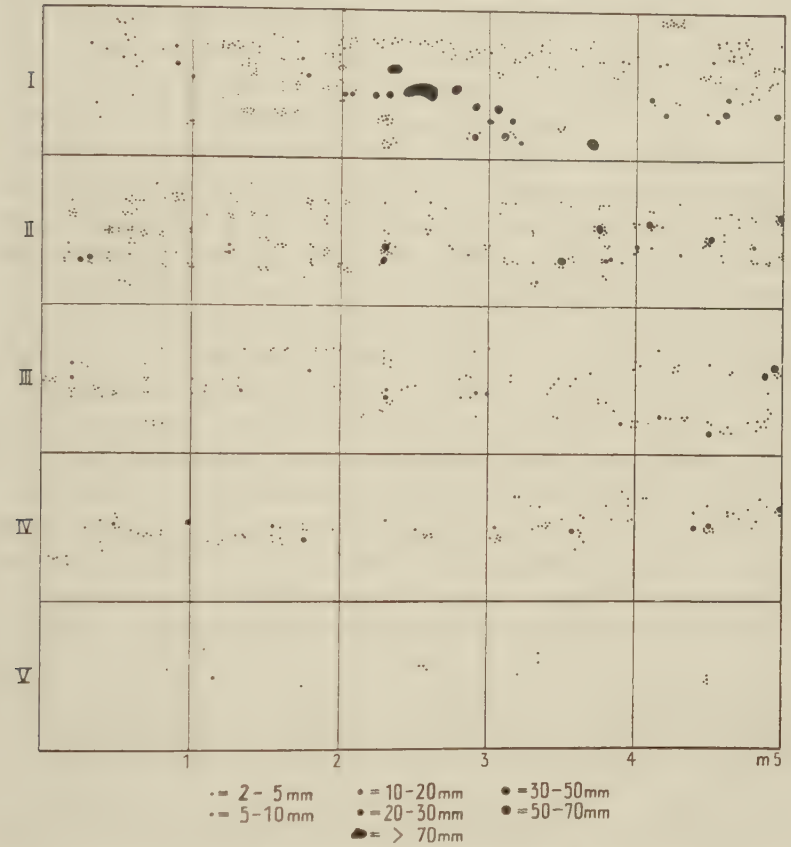

Fig. 8. Durchwurzeltes Bodenprofil hintereinander gestaffelter Gräben. I = Graben in 1,50 m, II in 4 m, III in 7 m, IV in 10 m und V in 12 m Abstand von den Eichen. Die Grösse der Punkte entspricht den einzelnen Klassen der Wurzeldicke.

tung sehr unregelmäßig. Das voranstehend beschriebene Wurzelsystem von *Quercus rubra* glich weitgehend dem von *Quercus macrocarpa* auf lehmhaltigem Boden. Auch *Quercus macrocarpa*

entwickelt nach Weaver und Kramer[16]) sehr zahlreiche von der Hauptwurzel abzweigende Seitenwurzeln, die teils schräg abwärts, teils aufwärts wachsen und ein grosses Bodenvolumen einnehmen.

VI. BESPRECHUNG DER ERGEBNISSE

Als Repräsentant der in den Hecken vielfach verwendeten Standbäume wurde die Eiche herausgegriffen und ihre Wirkung auf die in nächster Nähe angebaute Kulturpflanzen untersucht. Die Schäden, die sich im Bereich der Bäume zeigten, waren auf mikroklimatische und biotische Einflüsse zurückzuführen. Während die Temperaturverhältnisse in Baumnähe nur wenig Änderung erfuhren, wurde die Feuchtigkeitsspendung in weit höherem Maße beeinflußt. Je näher die Pflanzen unter den Schirm der Baumkronen rückten, desto geringer war die ihnen zugute kommende Niederschlagsmenge. Dies galt sowohl für den zu Boden fallenden Regen wie auch für den nachts an den unterkühlten Pflanzen ansetzenden Tau. Die Wasserbilanz erfuhr eine weitere Verschlechterung dadurch, daß die an sich schon verminderte Bodenfeuchtigkeit in Baumnähe nicht den hier wachsenden Pflanzen allein zur Verfügung stand. Durch die Gehölzwurzeln fand ein erheblicher Wasserverbrauch statt, der in 2–4 m Entfernung von den Eichen bis zur Hälfte des ausnutzbaren Bodenwassers betrug. Je weiter die Probeentnahmestellen von den Bäumen entfernt waren und damit aus der Regenschattenzone herausrückten, desto höher lagen die Werte für den Bodenwassergehalt. Dennoch blieb ein Unterschied in den Feuchtigkeitsprozenten zwischen dem Acker mit durchschnittenen und unbeschädigten Gehölzwurzeln bis zu 12 m Eichenabstand erhalten. Grabungen, die am Ende der Vegetationsperiode vorgenommen wurden, bestätigten den engen Zusammenhang zwischen Bodenfeuchtigkeit und Durchwurzelung. Im Ackerland mit intakten und durchschnittenen Gehölzwurzeln war der Wassergehalt etwa von Parzelle 6 an (= 11 m Entfernung von den Eichen) gleich hoch. Diese Übereinstimmung beruhte auf einer raschen Abnahme der Wurzelzahl. Im Bodenprofil wurden hier an der Stichwand eines 5 m langen und 1 m tiefen Grabens nur noch 14 Wurzeln gezählt, denen 327 in 1.5 m Abstand von der Stammbasis der Eichen gegenüberstanden.

Als Indikator für die schlechteren Lebensbedingungen mit der

Annäherung an die Bäume konnte die Wachstumsleistung gelten. Wuchshöhe und Ernteertrag sanken ständig ab, je mehr die Kulturen in der Einflußzone der Eichen lagen. Die Ursache hierfür war eine Störung im Wasserhaushalt. In Schönwetterperioden traten ausgedehnte Dürreschäden auf, die sich in vermindertem Aufgang der Saat und später im Welken der Blätter äußerten. Das besonders schlechte Auflaufen des eingesäten Mohns war außerdem auf eine Keimungshemmung zurückzuführen, die bei einigen Pflanzenarten durch Eichenlaub verursacht wird. Auffällig war ferner die starke Chlorose, die bei Mais in den baumnahen Parzellen auftrat. Erhöhte Düngung vermochte die Schäden bis zu einem gewissen Grade einzudämmen, was sich in besserem Aussehen und günstigeren Erträgen äußerte. Das reichlichere Nährstoffangebot, das zunächst den Kulturpflanzen und nach dem Einwaschen in tiefere Bodenhorizonte auch den Baumwurzeln zur Verfügung stand, vermochte jedoch die Wirkung der Wasserknappheit in dieser Zone nicht zu kompensieren. Die Erträge stiegen erst dann merkbar, wenn die Hauptmasse der Wurzeln im Feldstreifen ihr Ende gefunden hatte, und sich damit der Bodenwassergehalt erhöhte. Wuchshöhe und Ernte ließen sich weitgehend verbessern, wenn die in das Ackerland hineinreichenden Gehölzwurzeln durchschnitten wurden. Die größere Vitalität der Pflanzen in den baumfernen Parzellen zeigte sich nicht nur bei den angebauten Kulturen, sondern auch in der Unkrautflora. Mit zunehmendem Abstand von den Eichen nahmen die Größe der Pflanzen und auch die Anzahl der Arten zu.

Es erhebt sich nun die Frage, wie weit auf Grund der vorliegenden Ergebnisse allgemeine Rückschlüsse bezüglich der Wirkung von Standbäumen in den Hecken zulässig sind, zumal die Angaben von W e n d t [17]) unseren Befunden zu widersprechen scheinen. W e n d t berichtet von der staatlichen Versuchsstation Retfala in Ungarn, daß der Erdbeerertrag im Schutz von 7–8 m hohen Eichen günstig beeinflußt wurde (Tabelle XV).

TABELLE XV

Erdbeerertrag mit zunehmendem Abstand von Eichen (nach W e n d t)

Entfernung in m	Ertrag in Gewichtseinheiten	Ernte in den ersten 10 Tagen in Gewichtseinheiten
6,6	10 155	2 115,5
14,2	9 375	1 782,5
19,6	8 475	1 005
26,3	7 362,5	780
32,6	5 012,5	560

Die besten Werte ergaben sich für den baumnahen Abschnitt. Diese Ertragsbestimmungen wurden aber erst in 6,6 m Entfernung von den Eichen vorgenommen. Es ist deshalb durchaus wahrscheinlich, daß der näher den Bäumen gelegene Abschnitt niedrigere Erträge aufwies. Leider wird auch nicht mitgeteilt, ob die Eichen unmittelbar am Feldrand standen oder von diesem durch einen Graben getrennt waren, oder ob durch besondere Maßnahmen die Wurzelentwicklung der Bäume in bestimmter Richtung beeinflußt wurde. An anderer Stelle geht Wendt auf die Bedeutung der Pappel in Windschutzanlagen ein. Er berichtet, daß selbst eine doppelte Düngung nicht den Schaden aufwiege, den diese Bäume im Acker verursachen (Tabelle XVI). Ebenso sei die Birke zum Anbau ungeeignet, da sie den Kulturpflanzen zu viel Nahrung entziehe.

TABELLE XVI

Ertragsmessungen für Roggen innerhalb und außerhalb des Pappelbereiches. Innerhalb des Pappelbereiches doppelte Düngung (nach Wendt)

Durchschnitt für die Ähren	Länge der Ähren in mm	Gewicht der Ähren in g	Anzahl der der Körner	Gewicht der Körner in g	Länge der Körner in mm	Dicke der Körner in mm
außerhalb	100,25	1,478	59,625	1,041	7,157	2,661
innerhalb des Pappelbereiches.	91,25	0,916	43,0	0,58	6,65	1,995

Umfangreiche Messungen über den Einfluß von Windschutzanlagen auf die Ackererträge führte Olbrich[8]) durch. Aus seinen Untersuchungen geht hervor, daß sich in Abhängigkeit von der Zusammensetzung, Art und Anlage der Hecken Ertragsdepressionen an den Feldrändern zeigten, wenn auch die Ernten im ganzen immer noch über denen der ungeschützten Flächen lagen.

Überall dort, wo zur Verhinderung von Erosions- oder mikroklimatischen Schäden Windschutzstreifen angelegt werden, wird man danach trachten, den unvermeidbaren Landverlust durch höhere Ernteergebnisse wettzumachen. Dabei hat man bisher kaum berücksichtigt, daß eine nicht unerhebliche unterirdische Beeinflussung der Kulturpflanzen durch die Holzwurzeln eintreten kann und bei der Auswahl der Gehölze im allgemeinen nur die natürlichen Gebüschformationen des betreffenden Gebietes als Vorbild benutzt (vgl. Jessen[4]), Troll[14]), Tüxen[15])). Man wird aber zur Verringerung der — auch nach anderen Autoren — fast überall auftretenden Ertragsschäden am Gehölzrand bei künstlicher Anlage von Hecken mehr als bisher auf die Ausdehnung der Wurzelsysteme der einzelnen Gehölzarten achten müssen. Es sind vorwiegend

solche Sträucher und Bäume auszuwählen, bei denen die gesamte Wurzelmasse gering ist oder sich mehr in vertikaler als in horizontaler Richtung ausdehnt. Auch werden sich Gehölze mit einem starken Wasserbedarf stets ungünstiger auswirken als solche mit geringerem Wasserbedarf. Eine völlige Ausschaltung der Wurzelkonkurrenz im Acker ist schwer durchführbar, eine weitgehende Einschränkung durch geeignete Maßnahmen aber durchaus möglich. W e r t h [18]) machte bei seinen Windschutzanpflanzungen auf nicht abgetorften Hochmoorböden bei Osnabrück die Erfahrung, daß die Wurzeln immer so tief in den Boden eindrangen, daß 20–30 cm breite, 40–50 cm tiefe Gräben das Eindringen der Baumwurzeln in die Obst- und Gemüsekulturen hinein verhinderten. Nur von der Moorbirke führt W e r t h an, daß ihre Wurzeln von Zeit zu Zeit abgestochen werden müssen, da sie auch in nicht gekalkten Bodenschichten wächst. S c h e e r e r [10]) empfiehlt zur Einengung des Wurzelsystems eine Versorgung der Heckengehölze mit Dünger. M a r q u a r d t [6]) gibt an, daß in den Wallhecken die Wurzeln weniger weit in das angrenzende Feld hineinreichen. Die eigenen Versuche zeigten, daß ein Durchhacken der Wurzeln am Feldrand günstige Auswirkungen hat. Das Auswerfen eines Grabens wird nicht unbedingt erforderlich sein, wenn durch einen Untergrundlockerer die Möglichkeit gegeben ist, auch tiefer streichende Gehölzwurzeln zu durchschneiden. Weitere Untersuchungen werden klären müssen, welche der vorgeschlagenen Maßnahmen zur Einengung des Wurzelsystems am vorteilhaftesten sind.

ZUSAMMENFASSUNG

1. Es wird die Wirkung der in Hecken häufig als Standbäume vertretenen Eichen (*Quercus rubra*) auf das anliegende Ackerland untersucht.

2. Die Luft- und Bodentemperaturen werden in Baumnähe nur wenig, die Feuchtigkeitsspendung durch Regen und Tau stark verändert. Die Bodenfeuchtigkeit stieg an, je weiter die Meßstelle aus der Regenschattenzone und dem von Gehölzwurzeln durchzogenen Bereich herausrückte. Der Bodenwassergehalt ließ sich steigern, indem am Feldrand die Baumwurzeln durchschnitten wurden.

3. Bei sämtlichen angebauten Kulturen nahm sowohl die Wuchshöhe als auch der Ertrag mit steigendem Abstand von den Eichen zu. Die Ernten waren in den Feldern höher, in denen die Wurzelkonkurrenz der Gehölze durch einen schmalen Graben aufgehoben war. Auch traten hier weitaus geringere Dürreschäden als in den von Wurzeln durchzogenen

Vergleichsfeldern auf. Es lassen zich demnach durch einfache kulturtechnische Maßnahmen Wuchshöhe und Ernteergebnis steigern.

4. In der Unkrautflora machten sich die schlechteren Lebensbedingungen in Baumnähe in einer Reduktion der Wuchshöhe der Unkräuter und Verringerung der Artenzahl bemerkbar.

5. Wurzelgrabungen ließen die Benachteiligung der baumnahen Parzellen deutlich erkennen. In 1,50 m Abstand von den Eichen wurden auf der 5 m langen und 1 m hohen Stichmauer eines Grabens 327 Baumwurzeln, in 12 m Entfernung noch 14 gezählt. Die maximale Reichweite im Acker betrug 16 m.

6. Es ist anzustreben, bei der Auswahl des Pflanzgutes für Windschutzstreifen Gehölze mit geringer oder vorwiegend vertikaler Wurzelausdehnung zu besorgen. Ein Durchschneiden der Wurzeln bereits vorhandener Bäume und Sträucher entlang des Feldrandes setzt die Schadwirkungen infolge Ausschaltung der Wurzelkonkurrenz im Acker erheblich herab.

SUMMARY

1. The effect of oaks (*Quercus rubra*), as hedgerow trees, on adjacent arable land has been investigated.

2. Air and soil temperatures were affected only slightly by the presence of nearby trees whereas moisture supply from rain and dew was considerably modified. Soil humidity increased with distance from the zone of rain-shadow and from the root-permeated area. The soil water content increased after cutting the roots at the border of the field.

3. The height as well as the yield of the cultivated crops increased with distance from the oak trees. Yields were higher on those plots in which the competition from the hedge-tree roots had been eliminated by digging a narrow trench. Drought damage was much smaller on these plots than on the control plots where the roots had not been severed. Consequently it is possible to increase crop height and yield by simple cultivation measures.

4. The poorer conditions for plant growth in the vicinity of the trees were perceptible in the weed flora by a reduction in both height growth and number of species.

5. The presence of large numbers of tree roots in the plots adjacent to the trees was demonstrated by digging out the roots. 327 tree roots were counted at a distance of 1.50 m from the oak trees in a profile 5 m in length and 1 m in depth. At a distance of 12 metres from the oak trees this number had become 14. The maximum horizontal extension of the tree roots was 16 m.

6. It is recommended that trees having a predominantly vertical root system be selected as planting material for shelter belts. When trees or bushes are already present, cutting of lateral roots along the border of the field may diminish the damaging effect by reducing root competition in the field.

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OBSERVATIONS ON MIXED CULTURES OF NITROSOMONAS AND HETEROTROPHIC SOIL BACTERIA

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It has always been considered a difficult task to isolate the nitrifying bacteria in pure culture. The difficulty consists in getting rid of heterotrophic soil bacteria that seem to adhere strongly to the nitrifiers. The question has therefore been raised whether a sort of symbiotic relationship exists between the nitrifying bacteria and certain heterotrophic micro-organisms in the soil. However, no one has as yet succeeded in proving clearly that so is the case. Kingma Boltjes [5]) investigated a small bacterium which was identified as *Hyphomicrobium vulgare* and frequently was seen on mineral silica gels in association with *Nitrobacter*. By the use of a micromanipulator Kingma Boltjes succeeded in isolating the nitrifier. Imsenecki [3]) found that a myxobacterium developed together with nitrifying bacteria when silica gels were inoculated with soil particles. The myxobacterium was given the name *Sorangium symbioticum*. Growth of the nitrifying bacteria took place initially but was followed by autolysis of the cells when the myxobacterium later became the dominating organism. Imsenecki calls this phenomenon a symbiosis, but according to general terms it should merely be called a metabiosis, a rather common phenomenon in nature. Pandalai [7]) cultured *Nitrosomonas* together with *B. megaterium*, *B. mycoides*, *Azotobacter chroococcum* and other bacteria, and found in all cases enhanced nitrification in his mixed cultures. No data were, however, published. Stapp [9]) isolated several heterotrophic soil bacteria

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from enrichment cultures of nitrifying bacteria. With one exception, all of them were pigment producers of the *Bacterium*- and *Pseudomonas*-type. Three species were isolated from ammonia-oxidizing bacteria (*Nitrosomonas*) and four from nitrite-oxidizing (*Nitrobacter*). These heterotrophs were extremely tolerant towards high concentrations of ammonia and nitrite; even in a 30 per cent ammonium sulphate medium growth was visible, and one (a *Pseudomonas*) tolerated 2 per cent sodium nitrite in the medium. In inorganic media the viability of the heterotrophic bacteria was higher in the presence of nitrifiers than when in pure culture. Growth of the heterotrophs associated with the *Nitrosomonas*-group was not accelerated when cultured together with *Nitrosomonas*, whereas growth of the heterotrophs from the *Nitrobacter*-group were so when cultured together with *Nitrobacter*. Stapp also found accelerated nitrification in mixed cultures of these bacteria. As different investigators always find different heterotrophic bacteria adhering to the nitrifiers, Stapp does not believe in a specific action on the nitrification process, *i.e.* there is no reason to believe in a true symbiosis between nitrifiers and heterotrophic bacteria. The author (Gundersen [1] [2]) found that heterotrophic soil bacteria isolated from enrichment cultures of nitrifiers were able to neutralize the toxic effect of peptone, phenylalanine and tyrosine on *Nitrosomonas* when in mixed culture. This observation could possibly explain why nitrification can take place rapidly in soil and even in farmyard manure (Jensen [4]) in presence of considerable quantities of organic matter. In pure cultures these autotrophic bacteria are very sensitive to a variety of organic compounds, though not equally to all.

The present investigation comprises some observations made on mixed cultures of *Nitrosomonas* and heterotrophic bacteria from enrichment cultures of the nitrifier.

EXPERIMENTAL

Methods of enrichment and isolation of bacteria

A small sample of garden soil (from the University Botanical Garden, Copenhagen) was added to a 300-ml flask containing 25 ml of a basal mineral medium (Winogradsky's ammonia medium, in the sequel designated WAM). The medium was made

up of $(NH_4)_2SO_4$, 4 g; $MgSO_4.7\ H_2O$, 0.125 g; NaCl, 0.125 g; $FeSO_4.7\ H_2O$, 0.0025 g; $MnSO_4.4\ H_2O$, 0.0025 g; Hoagland trace mineral solution 1 ml, and tap water 1000 ml. To each flask a small spatula of calcium carbonate was added. The media were autoclaved at 115°C for 20 min. Final pH was 8.0 (glass-electrode). All cultures were incubated at 28°C.

Successive transfers (with five-day intervals) of 1 ml of culture fluid resulted in accumulation of ammonia oxidizers of the *Nitrosomonas*-type. After about 30 days one drop of the last enrichment culture showing vigorous nitrite reaction with the Griess-Ilosvay reagent was transferred to six test tubes containing 4 ml of the same medium. These cultures were incubated 1, 2, 3, 4, 5 and 6 days respectively, and then diluted from 10^{-1} to 10^{-6} in WAM and again incubated. It was hoped that this procedure would result in obtaining a pure culture of the nitrifying bacterium, as it might be expected that the nitrifier at one moment or other would exceed the heterotrophic bacteria in cell numbers. This proved not to be the case. At all dilutions where nitrite reaction was positive, heterotrophic bacteria were also present, as shown by tests on nutrient agar and broth. The nitrite-negative cultures were all sterile. Plating on nutrient agar and subsequent isolation showed that three species of heterotrophic bacteria always accompanied the nitrifier. The heterotrophic bacteria (in the following designated H–40, H–41 and H–43) were studied in pure culture.

H–40 appeared to be a non-fluorescent *Pseudomonas*. Its main characteristics are: In broth gram-negative regular rods, 2 to 3 by 0.5 μ, motile by single polar flagella (Fig. 1). Aerobic as well as anaerobic growth. Acid but no gas from maltose. No acid and no gas from glucose, fructose, saccharose, arabinose, mannitol, lactose and glycerol. Litmus milk acidified and coagulated in 9 days. Indole not produced. Gelatine not liquefied. Starch not hydrolyzed. H_2S not formed. Agar colonies circular, 1–2 mm (5 days), smooth, slightly convex, whitish or opalescent. Broth turbid with small white sediment. Potato, smooth, colourless colonies becoming brown after 9 days.

H–41. *Pseudomonas* (*ambigua?*). From agar it appeared as small gram-negative short rods or cocci, 1 to 2 by 0.5 μ, rods sometimes pointed at one end. Motile by single polar flagella (Fig. 2). Aerobic. No spore-formation. Acid but no gas from arabinose. No acid or

gas from glucose, fructose, saccharose, maltose, lactose, mannitol and glycerol. Litmus milk not attacked. Indole and H_2S not formed. Starch not hydrolyzed. Gelatine not liquefied. Agar colonies 0.3–0.6 mm after six days, circular, convex, white, smooth. Poor growht in broth, even after 14 days of incubation. Potato, good growth, colonies 0.5–1.0 mm, circular, convex, smooth, whitish becoming light brown on ageing.

H–43. From agar small irregular, none-sporeforming, gram-negative cocci, occuring singly or in pairs, 0.5 by 0.3 to 0.4 μ (Fig. 3). Motile. Aerobic, facultative. No acid or gas from glucose, fructose, maltose, saccharose, arabinose, lactose, mannitol and glycerol. Gelatine and litmus milk not attacked. No indole or H_2S produced. Starch not hydrolyzed. Agar colonies 0.5 mm in 9 days, circular, white, convex, hard and difficult to remove from the agar surface. When seen from underneath in thin agar layers the colonies appear as white rings. Broth turbid, with small finely granular sediment, no ring or pellicle. Potato, flat, thin growth, moist, colourless. On asparagin-lucerne-extract agar star-like aggregates of 3 to 20 cells are formed; the individual cells seem more elongated than on nutrient agar. This micro-organism probably is the "Salpeterpilz", *Hyphomicrobium vulgare*, which was isolated from crude cultures of nitrifying bacteria and described by Stutzer and Hartleb[10]) and later recognized by Kingma Boltjes[5]) in cultures of *Nitrobacter*.

Inorganic nitrogen-metabolism of the heterotrophic bacteria

The behaviour of the heterotrophic bacteria towards ammonia, nitrite and nitrate is of special interest. The results of a series of tests in different liquid media containing the three inorganic ions are summarized in Table I.

None of the heterotrophs are able to oxidize ammonia no nitrite or to nitrate. When 0.5 per cent glucose is added to the inorganic medium at pH 7.3, H 40 is able to use ammonia, nitrite and nitrate as nitrogen sources. H 41 and H 43 will not grow during a 30 days incubation periode in these media. Growth was estimated turbidimetrically. In diluted broth H–40 reduces nitrate to nitrite and ammonia, and nitrite to ammonia, H–41 reduces nitrite but not nitrate, and H 43 removes nitrite quantitatively from the medium; ammonia could not be detected.

TABLE I

Inorganic nitrogen metabolism of heterotrophic bacteria					
Medium	Days of incub.	Ion init. present	Bacterium		
			H–40	H–41	H–43
			Ion recovered		
Inorganic (WAM).	17	NH_4	NH_4	NH_4	NH_4
Broth, diluted	20	NO_3	NO_2 / NH_4	NO_3	NO_3
id.	20	NO_2	NH_4	NH_4	?
			Growth (turbidimetric)		
Inorganic (WAM) (minus $CaCO_3$) plus 0.5% glucose.	30 *)	NH_4	100	0	0
id.	30 *)	NO_2	58	0	0
id.	30 *)	NO_3	50	0	0

*) Growth of H–40 estimated after 9 days.

All three heterotrophs are able to survive for 36 days in WAM, also when in pure culture.

Mixed cultures of Nitrosomonas and heterotrophic bacteria in liquid medium

Although growth of heterotrophic bacteria and *Nitrosomonas* in the basal medium causes no visible turbidity of the liquid even after weeks of incubation, plate counts on nutrient agar and on silica gels show that cell multiplication nevertheless takes place. Table II shows typical results of plate counts as compared with nitrite production by *Nitrosomonas*.

TABLE II

Growth of heterotrophic bacteria in association with *Nitrosomonas*				
Days of incubation	Cell number/ml			NO_2–N, μg/ml
	H–40, $\times 10^4$	H–41, $\times 10^5$	H–43, $\times 10^5$	
0	0.6	4.5	3.3	0.8
3	22.6	190	170	14
7	400	445	248	103
16	400	230	200	230

As noticed by several workers, the development of bacteria seems to be restricted to the surface of calcium carbonate particles which make up the main part of the bottom deposit in the cultures. The supernatant clear medium is very poor in bacteria, whereas in the sediment cells are embedded in large quantities, as will be

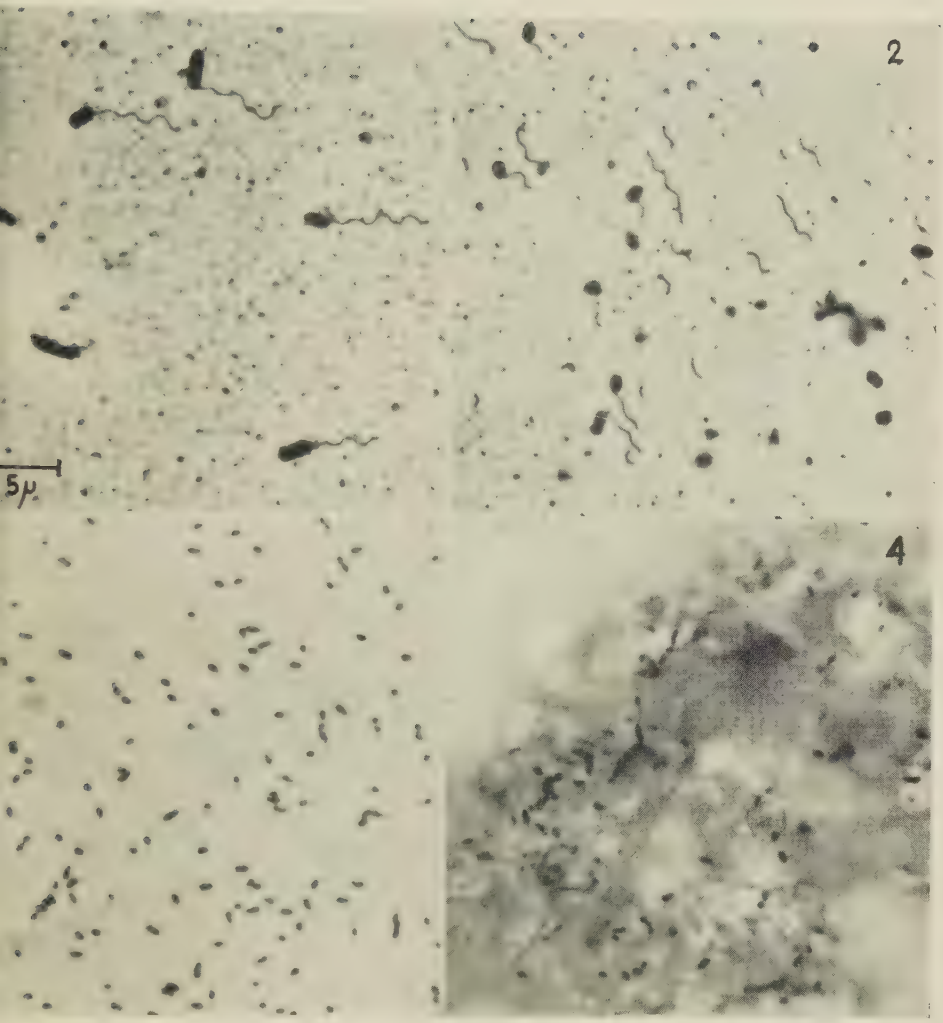


Fig. 1. H–40 from nutrient broth 3 days at 28°.
Fig. 2. H–41 from potato 7 days at 28°.
Fig. 3. H–43 from nutrient broth 5 days at 28°.
Fig. 4. Population of heterotrophic and nitrifying bacteria sited on sediment of calcium carbonate in inorganic ammonia medium. 3 days at 28°.

Fig. 5, 6 and 7. Cell aggregates from mixed cultures of *Nitrosomonas* and heterotrophic bacteria in inorganic ammonia medium. 14 days at 28°.

seen in Fig. 4. In older cultures thick masses of cells are frequently seen on the carbonate particles. Fig. 5, 6 and 7 show characteristic small aggregates or microcolonies from bottom deposits of a 14 days old culture in WAM. The cells are stained according to the flagella-staining method of Leifson[6]). Cultures were first shaken vigourously for about one minute, and a drop of the suspension thus obtained was transferred to a clean slide before staining. Cells of H–40 are readily recognized, whereas H–41 and *Nitrosomonas* could not be recognized with certainty. The rods with a long flagellum, forming star-like microcolonies seem to be *Hyphomicrobium vulgare* (H–43). It will be seen that the end of the flagella forms a loop or a bud which is characteristic for this organism.

Mixed colonies on silica gels

Silica gels were prepared according to Winogradsky (see Pochon[8])) from hydrochloric acid (dens. 1.10) and a sodium-silicate solution (dens. 1.06) and aliquots of 30 ml poured into 9-cm Petri-dishes. After coagulation the gels were dialyzed for 3 days in running tap water. Then 3 ml of a tenfold concentrated WAM (minus calcium carbonate) was pipetted into the Petri-dishes and excess water allowed to evaporate in an electric oven at about 80° C. The surfaces of the gels were then sterilized under a UV-sterilamp for 10 min and subsequently inoculated by spraying with a dilution of an actively nitrifying culture of *Nitrosomonas* and the heterotrophic bacteria. The inoculated surface was finally covered with a thin layer of a sterile $CaCO_3$ suspension. After a few days in the incubator the surface becomes dry with powdered carbonate.

Production of nitrous acid by *Nitrosomonas* results in dissolution of the calcium carbonate, and after 7 to 10 days minute transparent points are seen in the white surface. Under a hand-lens these small colonies appear as homogeneous half-dissolved areas, much like melting snow. Two to three days later the calcium carbonate in the middle of the area becomes entirely dissolved, and a regular colony grows up. These colonies are at first clear as water but, within a few days, they become more and more yellow to brownish; frequently small secondary colonies are formed in the periphery. The primary as well as the secondary colonies are circular, slightly

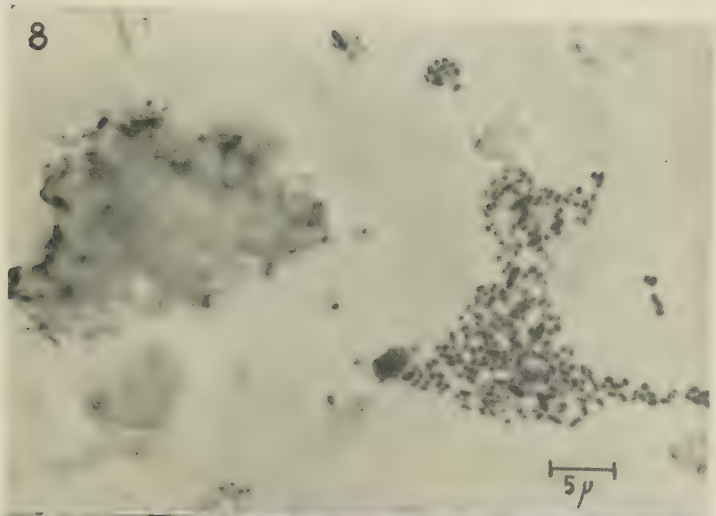
convex, smooth and glistening. Thus the colonies of these bacteria on silica gels macroscopically consist of two parts with sharp contrast; (1) the center which is the organized colony and where the calcium carbonate is entirely dissolved, and (2) a surrounding ring of half-dissolved carbonate (Fig. 10).

Contact preparations from young colonies and parts of older colonies were made by inserting softly the sharp-cut end of a thin wooden stick into the colony and quickly transfering the adhering material to a slide. After drying the slides were carefully stained either with toluidin blue or with crystal violet.

Fig. 8 and 9 show microphotographs taken from different parts of colonies. Different cell types, large and small rods and coccoid bacteria, have developed side by side, partly on the carbonate particles and partly in the dissolved interstices. It will also be noticed (Fig. 9) that bacteria have advanced to the solid carbonate outside the half-dissolved zone of the colony. Here vigorous growth results in large masses of cells adhering to the surface of the particles. Numerous attempts have been made to isolate *Nitrosomonas* in pure culture from different parts of these colonies but separation of *Nitrosomonas* from the heterotrophic bacteria was not successful. It is therefore evident that the development of all four bacteria, the nitrifier as well as the heterotrophic bacteria, takes place in close association, and that the morphology and the physiology of the colony must be the *summa summarum* of growth of four different species of micro-organisms "isolated" simultaneously from soil.

DISCUSSION

The development of different species of micro-organisms side by side as observed in these mixed cultures implies that they must thrive well together. No kind of antagonism could be present. They form a unit, a small community of living organisms. The question arises whether these cells cooperate in some way or other, *i.e.* that they live in symbiosis. This would be true if it could be shown experimentally that growth and metabolism was enhanced in mixed cultures as compared with pure cultures of the individual species, but the complexity of the problem makes it rather difficult to control conditions in the mixed cultures. Attempts



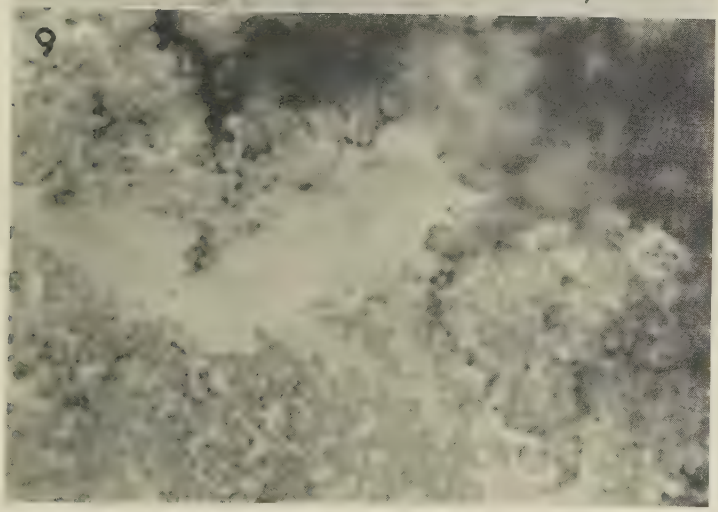


Fig. 8. Contact preparation from half-dissolved zone of young colony of *Nitrosomonas* and heterotrophic bacteria on silica gel. To the left, particle of calcium carbonate with adhering bacteria. 11 days at 28°.

Fig. 9. Contact preparation from border of half-dissolved zone and undissolved zone of silica gel colony. Black areas are clumps of bacteria on calcium carbonate particles. 7 days at 28°.

Fig. 10. Colony of *Nitrosomonas* and associating heterotrophic soil bacteria on silica gel (diagrammatic). 20 days at 28°. Note small secondary colonies.

have been made to demonstrate a stimulation of nitrificatrion (as measured by nitrite production) in mixed cultures, but the results obtained are not clear (Pandalai[7]); Stapp[9]); Gundersen[1) 2)]). With the present collection of "symbiotic" heterotrophs the estimation of nitrite production by *Nitrosomonas* in mixed cultures probably would not be reliable, since nitrite is metabolized by the heterotrophs.

It must be admitted that the apparent state of dependance between these micro-organisms could be explained in other ways. The difficulty of isolating *Nitrosomonas* in pure culture could be due to physical factors, for example adsorption of bacteria to solid particles ($CaCO_3$), slime or to zoogloeae formed by one or more species of the microorganisms. *Nitrosomonas* are known sometimes to be aggregated in zoogloeas; it has not been possible, however, to observe zoogloea formation in the strain taking part in the present experiments. But if adsorption phenomena really occur it would be difficult to separate the organisms by ordinary dilution and plating methods. In spite of insufficiency of the inorganic media to support heterotrophic growth, the heterotrophic bacteria would nevertheless develop to some extent on small impurities of organic matter always present in the water and the chemicals used.

SUMMARY

Naturally mixed cultures of *Nitrosomonas* and heterothrophic micro-organisms from soil have been examined. The autotrophic *Nitrosomonas* as well as heterotrophic bacteria would grow and multiply side by side in inorganic liquid media and also on silica gels where the micro-organisms form characteristic mixed colonies. The possibility that the micro-organisms make up a natural symbiotic unit or merely develop together owing to physical factors preventing a separation of the cells is discussed.

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THE LIBERATION OF AMINO ACIDS AND REDUCING COMPOUNDS BY PLANT ROOTS *)

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INTRODUCTION

The liberation of organic substances by roots of growing plants is of considerable economic and academic interest. In practical agriculture, the possible production by roots of substances which are toxic, stimulatory or essential to other plants and to parasitic, saprophytic or symbiotic soil micro-organisms, is of importance in relation to intercropping and crop rotation [1] [6] [7] [18] [21] [22]. Academically root "excretions" may be important considerations in ecological investigations relating to plant dominance and succession, in physiological work on root permeability, metabolism and growth and in microbiological studies on the incidence and function of parasitic and non-parasitic fungi, bacteria, nematodes and other organisms in the neighbourhood of the root [5] [8] [9] [12] [16] [18] [27]. Yet despite the broad areas of research in this field, surprisingly little work has been done in it. This may be due, in part, to the nature of the problem; the difficulty of distinguishing between "excretory" products of intact roots and products of breakdown and autolysis of sloughed off or dead root parts; interference by micro-organisms under natural conditions; maintenance of normal plant growth under aseptic conditions; and detection, identification and estimation of small amounts of active substances. The advent of partition paper chromatography has simplified at least this last problem and it is likely that extensive application of this technique will contribute significantly to the study of root excretion [10] [13].

*) Contribution No. 385

Since much of the evidence for and against the liberation of organic substances by roots has been summarized in several reviews [2] [6] [18] [27], it will suffice perhaps to mention a few reports on the liberation of amino acids and reducing substances. Even in 1920 Lyon and Wilson [20] had shown that plants growing in sterile solutions liberated nitrogenous, reducing and oxidizing substances in amounts which suggested an actual excretion rather than breakdown of root tissues. As is well known Virtanen and his associates in Finland [30] [33] demonstrated that nodulated legumes secreted appreciable amounts of amino acids such as aspartic and β-alanine. The presence of more than two acids would be expected if they arose from sloughed off or dead tissue. No excretion was obtained with uninoculated legumes. Kandler [10] has reported liberation of amino acids by excised corn roots. Nutman [24] has suggested that coloured compounds resulting from a reaction between root excretions of certain plants and clay minerals may be due to amino compounds. Stolp [29] could obtain no evidence of amino acid excretion but claimed that mucoid materials were liberated by young roots; this may account in part for the observed increases in numbers of micro-organisms in the rhizosphere. Lundegårdh and Stenlid [19] have reported that nucleotides, flavanones and other reducing substances are produced by roots of peas and wheat. Brown and Robinson [4] demonstrated that exudates of roots of Sorghum seedlings promoted extension growth of root segments of peas and maize. The active substance was considered to be a pentose sugar or a closely allied substance. D-xyloketose was found to produce a similar effect. Stenlid [28] has presented evidence of the exudation of reducing materials from 3–4 day old excised wheat roots in response to inhibitors of aerobic metabolism. Excised wheat roots also appear to be able to liberate acetaldehyde, according to Nance and Cunningham [23].

Studies on the rhizosphere or zone of influence of the roots of growing plants have indicated that there is a preferential stimulation of various groups of organisms, particularly those requiring amino acids for maximum growth [11] [17] [25] [31] [32]. Amino acids may be produced in the rhizosphere in amounts which would permit growth of amino acid requiring bacteria by a number of agencies: excretion from intact roots; breakdown and autolysis of dead and

dying cells and root hairs and of sloughed off root fragments; decomposition of these root parts and of microbial protoplasm and, finally, through microbial synthesis, for there is some evidence that bacteria with simple nutritional requirements, also stimulated in the rhizosphere, liberate amino acids which can be used by the amino acid requiring bacteria [17]). Most recently [13]) it was reported that appreciable amounts of amino acids and small, but detectable, amounts of reducing substances were elaborated by plant roots in response to drying and remoistening. Since under field conditions plant roots are constantly subjected to changes in soil moisture significant amounts of amino acids and other substances may thus be liberated for use by the rhizosphere microflora, and especially, the amino acid requiring bacteria. The present paper deals with further studies on the production of amino acids and reducing substances by various plants in relation to desiccation and under aseptic conditions.

METHODS

Plants were grown in 5- or 9-inch pots containing thoroughly washed sand or a 1 : 1 sand-soil mixture moistened with dilute mineral solution and water respectively. Seeds were surface sterilized by momentary immersion in 95% ethyl alcohol, followed by treatment with 1 : 1000 mercuric chloride for 10 minutes. They were washed in sterile water, germinated on agar, and then transferred to weighed pots in the greenhouse. Dilute mineral solution and distilled water were added to the sand and sand-soil series respectively as required. For analysis, pots were removed at suitable intervals and divided into two lots, one of which was allowed to dry out and the other kept moist. When the plants in the former set showed signs of wilting all pots were adjusted to their original moisture content, the openings at the bottom being closed with clean stoppers. After one hour all pots were leached with water, and the leachates (amounting to 200 ml solution) collected in clean glass jars. All solutions were filtered and stored in a deep-freeze unit; samples for analysis were removed as required, concentrated by freeze-drying and the residue taken up in 10% n-isopropyl alcohol. Suitable amounts of this solution were placed on Whatman No. 4 filter paper for ascending chromatography with 75% ethyl alcohol as solvent; after 18–20 hours the papers were removed and dried. One set was sprayed with ninhydrin (0.2% in ethyl alcohol), and developed at 45° C; one set was developed with isatin [26]), and one set sprayed with *p*-anisidine hydrochloride (saturated solution in n-butyl alcohol) and developed for 10 minutes at 105° C. Suitable aliquots of the isopropyl alcohol solution were also analyzed for amino nitrogen with chloramine-T [14]) in a conventional Warburg apparatus.

Sterile plants were grown in small units as described by Blanchard and Diller[3]). After abundant root growth had occurred the solutions were removed aseptically, tested for sterility and the sterile solutions treated as were the leachates described above. Since the amount of amino nitrogen from individual units was very small, the contents of two or more were pooled, prior to freeze-drying.

Aliquots of representative leachates were also neutralized and dispensed into small test tubes, glucose added to give a 0.1% solution and sterilized. These tubes were inoculated with selected amino acid requiring bacteria isolated from soil.

RESULTS

Liberation of amino acids and reducing substances by plants in sand cultures

It may be observed in Table I that significant amounts of amino nitrogen were recoverable in the leachates of sand which had been dried until the plants had begun to wilt, and remoistened.

TABLE I

Liberation of amino acids by plant roots in sand in relation to drying

Leachate obtained from	Amino nitrogen *) (μl CO_2)	
	Seedling stage	Flowering stage
Peas, normal moist sand	72	0
,, dried, remoistened sand	104	36
Soybean, normal moist sand	0	60
,, dried, remoistened sand	60	120
Wheat, normal moist sand	288	—
,, dried, remoistened sand	480	—
Barley, normal moist sand	0	244
,, dried, remoistened sand	42	1680
Tomato, normal moist sand	40	0
,, dried, remoistened sand	88	80

*) In 200 ml leachate, after subtraction of reagent blank values.

These plants all recovered from the treatment. Wheat and barley liberated considerably more amino nitrogen than the other plants; no particular relationship between age of plant and liberation of nitrogenous material is apparent except with barley. Of interest too

Fig. 1. Paper chromatogram indicating the liberation of amino acids by roots of soybean in sand in relation to drying.

1. Seedling stage, normal moist sand. 2. Seedling stage, dried, remoistened sand. 3. Flowering stage, normal moist sand. 4. Flowering stage, dried, remoistened sand. 5. Amino acid mixture ascending: lysine, asparagine, aspartic, glutamic, proline, leucine. 6. Casamino acids.

is the fact that certain plants, even in moist sand, also liberated detectable amounts of amino nitrogen. Leachates from sand in pots without plants, but treated identically, yielded no amino acids. These data agree in general with results published earlier [13]) and are supported by chromatographic evidence as shown in Figures 1 and 2. In every case there is a distinct difference in amino-nitrogen content of leachates between the dried-remoistened series and that which had not been dried. A variety of acids has been distinguished by the techniques used: glutamic and aspartic,

proline, leucine, alanine, cysteine, glycine, lysine and phenylalanine. Further substantiation of these results was afforded by the observation that distinctly better growth of four cultures of amino-acid requiring bacteria occurred in leachates of the dried-remoistened series as may be seen in Table II.

TABLE II

Growth of amino acid requiring bacteria from soil in leachates from sand cultures of various plants

Leachate obtained from	Cultures *)			
	1	2	3	4
Wheat, normal, moist sand (1)	0	±	0	0
,, ,, ,, ,, (2)	0	0	0	±
,, dried, remoistened sand (1)	±	+	+	+
,, ,, ,, ,, (2)	±	±	+	+
Barley, normal, moist sand (1)	0	±	+	±
,, ,, ,, ,, (2)	0	±	±	±
,, dried, remoistened sand (1)	+	±	++	++
,, ,, ,, ,, (2)	++	+	++	++
Oats, normal, moist sand (1)	0	0	0	±
,, ,, ,, ,, (2)	0	0	±	±
,, dried, remoistened sand (1)	+	+	++	++
,, ,, ,, ,, (2)	+	+	++	++
Tomato, normal, moist sand (1)	+	0	0	±
,, ,, ,, ,, (2)	0	0	±	±
,, dried, remoistened sand (1)	±	+	+	+
,, ,, ,, ,, (2)	±	±	+	±
Soybean, normal, moist sand (1)	0	0	0	0
,, ,, ,, ,, (2)	0	0	0	0
,, dried, remoistened sand (1)	±	+	+	+
,, ,, ,, ,, (2)	±	+	+	+

*) 0 no growth
± trace
+ fair to moderate
++ good

The presence of reducing substances, one of which may be glucose in leachates from the dried remoistened set of plants, is also apparent in Fig. 3. Another compound with an R_f value somewhat greater than glucose also is present. This may be a pentose as both are coloured purplish with *p*-anisidinehydrochloride and occupy approximately the same position. A third reducing compound appears in the soybean leachate below the "glucose" spot.

Fig. 2. Paper chromatogram showing the liberation of amino acids by roots of oats in sand in relation to drying. See legend Fig. 1.

Liberation of amino acids by wheat in soil-sand cultures

The wheat was grown in 9-inch pots until the flowering stage. Pots without plants were maintained as controls. Both sets of

TABLE III

Liberation of amino acids by wheat roots in modified soil in relation to drying	
Leachate obtained from	Amino nitrogen *) (μl CO_2)
1. Normal, moist soil	21
2. 1. with plants	32
3. Dried, remoistened soil	35
4. 3. with plants	247

*) See footnote Table I. Average of duplicates.

pots were then divided into two lots and treated as described above. A summary of representative data appears in Table III and in Fig. 4. A marked increase in amino nitrogen or amino acids in the leachates of the dried-remoistened series is evident. Again a variety of amino acids is liberated, particularly glutamic, aspartic, alanine, leucine, proline, and several others in smaller amounts.

Fig. 3. Paper chromatogram of reducing substances produced by roots of soybean and barley in sand in relation to drying.

1–4. *Soybean*: 1. Seedling stage, normal, moist sand. 2. Seedling stage, dried, remoistened sand. 3. Flowering stage, normal, moist sand. 4. Flowering stage, dried, remoistened sand.

5–8. *Barley*: 5. Seedling stage, normal, moist sand. 6. Seedling stage, dried, remoistened sand. 7. Flowering stage, normal, moist sand. 8. Flowering stage, dried, remoistened sand.

9. Glucose.

Amino acids and reducing substances in sterile solutions

Preliminary experiments with wheat and peas grown aseptically had shown that ninhydrin-positive substances were present in the mineral solution, though in very small amounts. Even these, however, stimulated growth of the amino acid requiring bacteria used earlier. When larger amounts of the concentrates of the sterile

Fig. 4. Paper chromatogram showing the liberation of amino acids by roots of wheat grown in a sand-soil mixture.

1. Normal moist soil. 2. Dried, remoistened soil. 3. Mixture of amino acids (Fig. 1, no. 5). 4. Casamino acids.

solutions were applied to paper for chromatography, two distinct ninhydrin-positive spots were produced by peas but only a faint

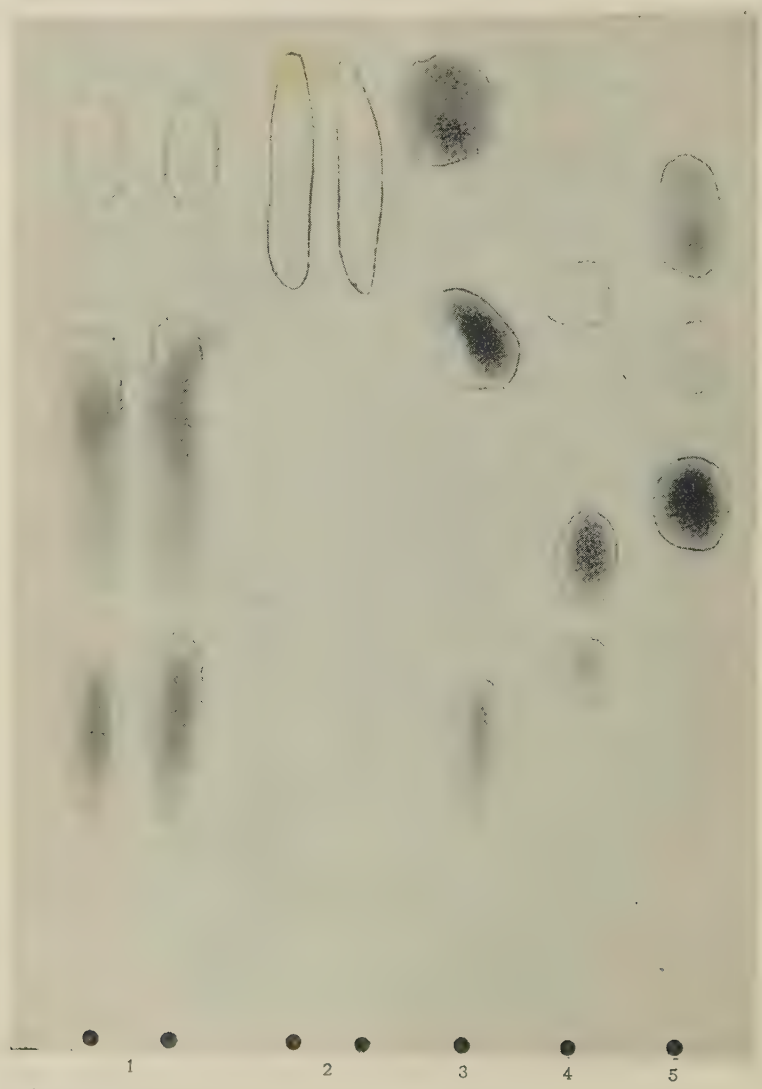

Fig. 5. Paper chromatogram of ninhydrin-positive substances produced by roots of peas and wheat grown aseptically.

1. Pea roots. 2. Wheat roots. 3–5. Amino-acid mixtures ascending: 3. Histidine, alanine, leucine. 4. Aspartic acid, glutamic acid, proline. 5. Serine, tyrosine, phenylalanine.

spot, in the approximate position of leucine was produced by wheat (Fig. 5). The latter, however, yielded a reducing compound with an *Rf* value similar to that of glucose.

DISCUSSION

The work reported in this paper was designed to explain, at least in part, the preferential stimulation in the rhizosphere or zone of influence of the roots of growing plants, of bacteria requiring amino acids for maximum growth. For these and other organisms in the rhizosphere clearly it matters little how substances such as amino acids and carbohydrates are made available to them; the root is only one of several sources. It has been amply demonstrated, however, that when roots in sand or sandy soil are dried and remoistened, appreciable amounts of amino acids and detectable amounts of reducing compounds are liberated and that these permit growth of amino acid requiring bacteria in pure culture. It is not unlikely therefore that in field soil, subjected to frequent drying and moistening, this phenomenon also occurs, thus providing the rhizosphere microflora with a food supply and especially with amino nitrogen. The results given in Tables I and III show too, that even under conditions of favourable moisture, detectable, and with certain plants, appreciable quantities of amino acids are liberated. This is true also for pea plants grown aseptically and to a much smaller degree for wheat.

No attempt was made in these experiments to distinguish between an excretory process as possibly a normal physiological function of intact roots and the liberation of amino acids and other soluble substances as a result of physical damage, sloughing off and autolysis of root fragments such as cortical and epidermal cells, root caps and root hairs. In the case of plants grown in moist soil or aseptically excretion, death and breakdown, or sloughing off of root parts may be responsible for the appearance of the amino acids observed, although according to Lyon and Wilson [20] the quantity of organic material liberated by roots growing aseptically in 6-litre flasks was sufficiently high to be attributable in part at least to excretion. The liberation of amino acids in the observed amount and variety by plant roots in response to drying and remoistening may be due to several factors. They may be

produced as a result of death and plasmolysis of the root cells themselves; they may move to the root surface during the drying process, and be washed off when water is added, and they may be leached out on remoistening as a result of rupture of the outer layers during drying. The increase in α-amino acids in plants as a result of proteolysis during wilting [15]) may contribute to an amino-acid imbalance resulting in an increased tendency to move outward, as has been demonstrated with nodulated legumes [30]).

Other points of interest deriving from the preceding observations concern the quantitative evaluation of the specific amino acids and reducing materials liberated, the conditions for maximum production of these substances such as soil moisture content, nature of the soil, age and kind of plant, and the relationship between liberation of amino acids under these conditions and the incidence of amino acid requiring bacteria in the rhizospheres of-different plants. These problems are being investigated further.

SUMMARY

Drying and remoistening of different plants grown in sand and in a sand-soil mixture resulted in the liberation of appreciable amounts of amino acids and detectable amounts of reducing compounds. Small quantities of amino acids were produced even under normal conditions of growth. The amino acids produced could be utilized for growth by amino acid requiring bacteria isolated from soil.

Peas grown under aseptic conditions also yielded small amounts of ninhydrin-positive substances. Wheat under similar conditions produced less of such materials but in addition liberated detectable amounts of a reducing compound.

These results are discussed in relation to the incidence of amino acid requiring bacteria in the rhizosphere.

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THE UPTAKE OF NUTRIENTS BY MATURE FOREST GROWTH

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ABSTRACT

The extremely low nutrient-status of various recently afforested moor soils, particularly Yorkshire (England) *Calluna* soils, raised the question of their ability to provide the possible nutrient-demands of continuous forest growth. This paper describes how, for calcium, potassium and phosphorus, uptake estimates have been calculated from existing nutrient-composition data, and discusses the silvicultural significance of such estimates, particularly in relation to nutrient-poor soils.

All existing nutrient-composition data for whole individual mature temperate forest trees are summarized: using yield-data and a method of calculation critically discussed, they are made to provide nutrient-uptake estimates for one acre of such forest after periods of 50 and 100 years' growth. Mean estimates representing "hardwood," "other conifer" and "pine" forest are then calculated showing: – the nutrients removed from the site via the various components of the timber-thinnings and clear-fellings, the

nutrients taken up and immobilized within the various component organs of the growing forest, and the total nutrient-uptake from the site.

The estimates show that timber exploited forest, by reason of its unavoidable continuous nutrient-removal from the site, differs fundamentally from unexploited virgin forest; in absolute terms this removal may be small, but its pedological and silvicultural importance upon any particular site, depends entirely upon the ability of the soil to replenish this loss. It is believed that up to now the failure to recognize this nutrient-removal upon nutrient-poor soils has diverted attention from an important factor initiating both soil-degradation and diminishing site-productivity.

Soil nutrient-data presented show that the nutrient-uptakes of timber-producing forest of either coniferous or hardwood species are so large compared with the nutrient-contents of moor soils that further overall soil-degradation and, sooner or later, diminished site-productivity are inevitable.

Upon such soils, therefore, continuous timber production cannot be sustained by ploughing or by the growth of hardwoods alone; new silvicultural techniques are needed which can restore to the site, by means of suitable soil-ameliorants and methods yet to be evolved, the nutrients continually being removed via the timber.

The paucity of knowledge concerning both the nutrient-demands of common tree species and the nutrient-status of the nutrient-poor soils upon which they are being extensively planted calls for an expansion of research upon these aspects if timber-production in this country is to be placed on a scientific, and not speculative, basis.

INTRODUCTION

Many chemical studies carried out upon British moor soils [41] [46] [47] [67], and in particular Yorkshire (England) *Calluna* soils [28] [56], have shown that the soils which are expected to support continuous forest growth and, in fact, a substantial part of this country's future timber reserves, are of very low nutrient-status, frequently having contents of important plant nutrients, either comparable to most unproductive soils elsewhere [21] [49] or lower than analagous soil types in other countries [1] [30] [34] [57].

As the continued growth of these forests depends upon the ability of these soils to provide continuously the nutrients required by forest growth, it seemed of some importance to enquire whether these low nutrient-contents were mere pedological curiosities or clear warnings that far greater attention should be given to the question of whether the possible nutrients required by this new and quite different form of land-utilization could, in fact, be provided by the soil.

It was first necessary, therefore, to have some idea of the quantities of important nutrients likely to be taken up by the growing forest and removed from the site via the timber.

The literature contained no comprehensive review of the nutrient-uptake estimates by mature forest growth, (E b e r m a y e r's uptake estimates [19]) being based on only single nutrient-composition studies for each of the three species pine, beech and spruce [27]) [63]) [76])), but did reveal conflicting views regarding their importance.

Thus, on the one hand, they were frequently stated to be small, especially when compared with those of agriculture, were being continually circulated via the leaf-fall, and that quite negligible quantities were removed via the timber [35]); on the other hand, it was stressed that the importance of nutrients to tree growth had been underestimated, and that deficiencies were possible through the absence of particular nutrients in the parent material [79]).

It was decided, therefore, to examine all the original studies on the nutrient-composition of mature forest trees, known to have been carried out [10]) [43]) [82]) and still referred to individually in recent studies [66]) [73]), to see how far they could give approximate estimates of nutrient-uptake by the forest, in respect of calcium, potassium and phosphorus, taking into consideration variations in uptake arising from differences in species, growth-rate, and soil conditions.

The estimates calculated were found to be of such general silvicultural importance and pedological interest, particularly upon nutrient-poor soils, that this paper was prepared to focus attention upon these neglected aspects of the soil-plant relationship.

This paper presents nutrient-uptake estimates for one acre of forest after 50 and 100 year growth periods, explains how they were calculated from the original data, critically discusses the validity of both the original data and the estimates, and discusses the silvicultural significance of such estimates, particularly in relation to nutrient-poor soils.

DEFINITION OF TERMS

Stem timber:	all timber exceeding 7 cm diam. overbark; made up of stemwood plus stembark.
Brush:	all timber less than 7 cm diam. overbark; made up of brushwood plus brushbark.
Timber:	stem timber plus brush.

Roots:	all root organs; including rootwood and rootbark.
Whole tree:	all aerial plus all subterranean organs.
Main growing crop:	a typical acre of the growing forest; reference may be made to the whole tree, stemtimber, brush, foliage, or roots.
Total thinnings:	the sum of the normal thinnings removed from a typical acre of main growing crop up to a particular age; reference may be made to the stemtimber or brush.
Clear-felling:	a felling of the entire main growing crop.
Rotation:	the number of years from establishment to clear-felling.
Quality-class:	a term used in Timber Yield Tables to distinguish different growth-rates of a particular species; the higher the quality-class, and smaller the quality-class number, the faster the growth-rate, and hence, rate of timber production.

THE NUTRIENT-UPTAKE ESTIMATES CALCULATED

Managed forest is made up of two principal parts, a main growing crop upon the site, and timber thinnings removed periodically from the site. The main growing crop is made up of foliage, brush, stembark, stemwood and roots, and the thinnings usually of brush, stembark, and stemwood, all these component organs contributing in varying degree at different ages to the overall nutrient demand upon the site. At any time all timber may be removed by clear-felling.

Nutrient-estimates were required which would show the role of each forest organ as nutrient-immobilizers or removers, and not be invalidated by variations in forest management practice.

Each original study upon the nutrient-content of an individual tree of known growth-rate was made to provide an estimate of the absolute weight of calcium, potassium and phosphorus and very occasionally nitrogen, contained within each component organ of the main growing crop and the total thinnings within one acre of forest of the particular species. The original trees varied considerably in age; to render the derived estimates comparable, each was calculated for two growth periods of 50 and 100 years, partly because these periods most closely resembled the ages of the original trees, and partly for their general silvicultural suitability.

The numerous individual estimates, shown in Table XI, were condensed in two ways; firstly, mean estimates were calculated for

the three groups of species (i) hardwoods, (ii) other conifers and (iii) pines; and secondly, under the four categories:

(i) nutrients removed from the forest-site via the total thinnings,
(ii) nutrients removed from the forest-site upto and including clear-felling,
(iii) nutrients taken up from the soil and immobilized within the organs of the main-growing crop,
(iv) total nutrient-uptake from the site (excluding litter) *i.e.* (i) plus (iii) above.

THE NATURE AND VALIDITY OF THE ORIGINAL DATA

The inaccessability and age of the original studies called for some consideration of their nature and validity.

The 42 original studies (see Table XI) were carried out principally from 1876 to 1893; they were concerned with nutrient-composition and uptake of the whole aerial, and sometimes subterranean, organs of temperate trees, mostly varying in age from 37 to 120 years, and always growing in closed canopy forest.

Age and quality-class of the tree sampled, locality and parent material were given; sometimes the soil profile was described and occasionally chemical soil analyses reported.

The tree sampled was representative of the average growth of the forest or plantation; it was felled, the timber organs sectioned into one metre lengths, and samples of known length removed for volume, fresh and oven-dry weight determinations, and subsequent chemical analysis: occasionally weight but not volume was determined. All investigators divided the timber into brush, stembark and stemwood, and most subdivided further: foliage was sampled when present.

Ashing of the several oven-dried samples was carried out in large platinum dishes at unspecified temperatures, 10 g crude ash sufficing for the determination of Ca, K, P, Mg, Na, Fe, S and Si; and occasionally Mn, Cl and Al. The crude ash was digested with HCl, taken to dryness to dehydrate silica, redigested and filtered: Ca was isolated from this filtrate as the oxalate and estimated gravimetrically as the ignited oxide; K was precipitated and weighed as the chlorplatinate, and P separated as magnesium ammonium phosphate and weighed as ignited magnesium pyro-

phosphate; only rarely was nitrogen determined. The results were expressed in various ways, but it was always possible to calculate the nutrient-concentrations and absolute nutrient-weights contained within each entire principal aerial organ of the sample tree. A summary of the original data is shown in Table XI. Some investigators calculated the nutrient-demands of the forest, and a few compared these demands with the nutrients present in the soil [26] [69]. Replicated samplings and analyses were rare, but this omission was, for an average picture, to some extent compensated by species being investigated more than once, and by the large number of subdivisions of the tree made prior to analysis; nevertheless, repeat investigations upon similar species of a similar quality-class were rare.

The accuracy of the chemical data was difficult to assess; for although the principles of the macrochemical procedures, in respect of the three elements were sound and were being widely used upon diverse materials [15] [74] at this time, more recent experience can suggest potential sources of error. Thus, rather carefully controlled ashing temperatures are necessary to retain all Ca, but especially K and P, and at the same time obtain a good-coloured ash free from organic matter; the absence of HNO_3 in the HCl extraction of the ash could incompletely dissolve some metals, and by incompletely dehydrating the silica, might permit the latter to contaminate subsequent precipitates; and again, the lack of an oxidative extract could permit incomplete precipitation of certain metals through the interference of organic matter.

Of all the element-values, only those for Fe, Mn and Si were thought high by Boresch [10], whilst curves prepared by Nemec [43] showed greater reproducability for Ca, K and P than Si, Cl and Mn.

Hence, unless there were consistent errors associated with all determinations of Ca, K and P, their estimation appears less prone to error.

HOW THE ESTIMATES WERE CALCULATED

The various steps of the calculation made for each original study may be readily explained by reference to a specific example, viz. the 144 year old specimen of *Abies alba* sampled by Weber [76].

(i) For this tree to have attained, at its age, the recorded stemtimber and

brush volumes of 3.28 and 0.26 cu.m respectively its growth-rate must have approximated continuously to Quality-Class I Schwappach [65]). Hence, after 50 years' growth, the timber-production of one acre of such forest would have been made up of:

(*a*) a main crop of 171 cu.m stemtimber plus 49 cu.m brush.

(*b*) total thinnings of 51 cu.m stemtimber plus 28 cu.m brush.

and after 100 years' growth:

(*c*) a main crop of 390 cu.m stemtimber plus 55 cu.m brush.

(*d*) total thinnings of 219 cu.m stemtimber plus 45 cu.m brush.

In certain original studies the stemtimber and brush volumes of the specimen tree had to be calculated from weight and specific gravity data, and other Timber Yield Tables [20]) [71]) [78]) used.

(ii) The 3.28 cu.m stemtimber and 0.26 cu.m brush of the sample tree contained certain absolute weights of nutrients shown in Table XI; assuming the nutrient-composition of these organs to be similar at the three ages, the absolute weights of nutrients contained in the above timber volumes were readily calculated.

(iii) The entire needles of the sample tree contained the absolute nutrient-weights shown in Table XI; at the particular age of the sample tree there were 142 trees per acre, hence the needle-nutrients per acre were readily calculated. By assuming similar nutrient-composition of needles at the three ages, but acreage weights of foliage in the proportions 133: 100: 66: 66 corresponding to the ages 37: 50: 100: 140+ years, the foliar-nutrients per acre at 50 and 100 years were calculated.

(iv) For the very few original studies sampling roots, on the average, of the total nutrients taken up by the sample tree, 13% were present in the roots. Hence, for all other studies, the nutrients contained in the entire organs of the main growing crop were calculated by multiplying the nutrient-weights contained in the aerial organs by 100/87.

(v) The following mean distributions of nutrients between stemwood and stembark were calculated from the original sample-tree data in Table XI, and were used to calculate the absolute nutrient-weights in these two organs from the mean stemtimber values for the three groups of species (also shown in Table XI):

Species group	% of stemtimber nutrient in the stembark		
	Ca	K	P
Pines	46	26	38
Other conifers .	63	47	60
Hardwoods .. .	70	33	45

(vi) A percentage distribution of nutrients among the various organs of the main growing crop was calculated for each uptake estimate of this type, but only the mean percentage distributions for each nutrient and species group are presented below (Table VII); the mean absolute nutrient-weights in the various organs of the main growing crop for each species group shown

in Table XI being calculated from these mean percentage distributions.

(vii) Certain hardwood species sampled by Henry, of unknown timber volume and unknown potential timber production, and of a shrubby nature, were omitted from the main estimates; for comparative purposes among themselves and because no other data for these species exist a very approximate uptake-estimate for a main growing crop at 37 years, was made by assuming 800 stems per acre.

(viii) A separate uptake estimate was made for an 8 year old crop of *Acer platinoides*, sampled by Schröder, by assuming 1,000 stems per acre.

THE VALIDITY OF THE ESTIMATES

The assumptions and possible errors associated with the various steps of the calculation are now considered.

(i) Timber Yield Tables of Schwappach [65]) were selected where possible because they included brush production, were more likely to be based on forest growth comparable to the sample-trees providing the original data, and, for most species, gave stemtimber volumes similar to those given in more recent Tables [78]).

The stemtimber and brush volumes used in each uptake estimate are shown in Table XI: for a few species of unknown growth potential, volume production for the nearest comparable species was taken (shown bracketed in Table XI).

(ii) By selecting growth periods of 50 and 100 years, for sample trees usually ranging from 37 to 120 years, the likelihood that a sample tree was at some stage growing and absorbing nutrients at a growth-rate greatly different from that shown by its development at the sampling-age was minimised.

(iii) The nutrient-concentration within particular timber organs was assumed to be similar at 50, 100 years and the sampling-age. The very few data on the variation of nutrient-composition of mature timber with age [75]) [81]) did not suggest any obvious correction for variation in age, and, as many of the sample-trees were aged very nearly 50 or 100 years, none was made. There was a possibility, however, that 100 year uptake estimates based on very much younger sample trees were somewhat overestimated, and 50 year estimates based on very much older trees somewhat underestimated.

(iv) Because water-free specific gravity varied among different specimens of the same species, the few estimates (Henry) where timber volumes of the sample tree were calculated from weight and other specific gravity values could be in greater error.

(v) The decreasing foliar-weights per acre with increasing age proportionality was a mean of observations made upon *Pinus silvestris* [37]), *Picea excelsa* [70]) and *Fagus sylvatica*, *P. excelsa* and *P. silvestris* [19]). Marked deviation from this mean could, of course, have no effect upon the estimates for the timber organs, and because the foliar-nutrients normally represented only a minor part of the uptake by the whole tree, could have little effect on the latter.

(vi) The estimates for the roots were the most problematical. They were calculated as a constant proportion of the total uptake, because (*a*) the few original studies including roots showed no obvious dependance of this proportion upon age of tree, and (*b*) quantitative studies [29]) showed approximately similar relative increases in timber and root volumes from 50 to 100 years for both pine and spruce. But as the root nutrients only represented a small part of the uptake by the whole tree, deviation from this proportion could not greatly affect the latter. The root-nutrient immobilization may have been consistently underestimated through the slow decay of root systems no longer forming part of the main growing crop.

Thus, individually the various assumptions could not greatly affect the overall uptake estimates, but collectively they could, and particular estimates might show appreciable cumulative error. But for many individual estimates and for the mean estimates representing the three species groups the variation in uptake seen would, in the main, be genuine and due to differences in species, growth-rate and site. All estimates excluded nutrients which may have been contained in the litter.

THE SILVICULTURAL SIGNIFICANCE OF THE MEAN ESTIMATES

The mean estimates presented below, and the conclusions reached, are of wide application, the reasons for this being presented in the next section.

(i) *Nutrients removed from the forest-site via the thinnings*

(*a*) the total quantities removed are shown in Table I.

TABLE I

Species group	Nutrients removed within the total thinnings, kg element per acre					
	During 50 years' growth			During 100 years' growth		
	Ca	K	P	Ca	K	P
Pines	35	15	4	88	35	9
Other conifers	56	26	5	164	82	13
Hardwoods	161	44	10	354	96	22

Clearly, the removal of timber thinnings necessitates the removal of nutrients from the forest site, and because of this is seen an important fundamental difference between a timber-exploited and an unexploited virgin forest, for in the latter the nutrient-demands of the forest are ultimately returned to the forest floor.

From data presented below (Table VIII) it is seen that after the

first 100 years' growth the nutrients removed from the site almost equal the nutrients immobilized within the main growing crop, hence the longer timber exploitation is continued the more is the overall nutrient-demand (by the forest) upon the site predominantly one of nutrient-removal from, rather than nutrient-immobilization within, the site, and the more does nutrient-removal from the soil become an increasingly important long term effect of forest growth upon the site.

The silvicultural significance of this nutrient-removal depends entirely upon the ability of the soil to replenish this continuous nutrient loss. Obviously, the nutrient-demands of unexploited virgin forest are considerably less than those for continuously exploited forest, but soils able to support the latter do exist. On the other hand, it is conceivable that certain soils support virgin but not exploited forest, because the extra nutrients required cannot be provided, hence the actual or previous existence of a virgin forest upon a particular site tells the forester very little about the long term timber-productivity of that site.

(*b*) the way in which the total quantities of nutrients removed via the thinnings are distributed among the three component organs of the thinnings.

Table II shows the percentage distributions of nutrients among the three thinning components, which, for each species group, are means of the several individual percentage distributions within that group.

TABLE II

Species group	Thinning component	Means of the percentage distributions of nutrients among the three thinning components					
		During 50 years' growth			During 100 years' growth		
		Ca	K	P	Ca	K	P
Pines	brush	65	66	75	43	49	55
	stembark	16	9	10	26	13	17
	stemwood	19	25	15	31	38	28
Other conifers	brush	76	73	77	45	44	52
	stembark	15	13	14	35	26	29
	stemwood	9	14	9	20	30	19
Hardwoods	brush	50	56	62	36	44	50
	stembark	35	15	17	45	18	23
	stemwood	15	29	21	19	38	27

Clearly, at least approximately half the total nutrients removed by any species group are contained within the brush, and of the remainder in the stem-timber, rather more than half the Ca, and rather less than half the K and P, are contained within the stem-bark. Hence, if the normally less commercially useful components of the thinnings viz., the stembark and brush are left on the forest floor, reductions of between 60 and 90% in the nutrient-removal via the thinnings are possible, without detriment to stemwood production; the older the thinnings the more important is the stembark, rather than the brush, in this respect.

(*c*) the nutrients removed via the thinnings for the production of one cu.m stemtimber are shown in Table III.

TABLE III

Species group	Nutrients removed in the total thinnings for the production of 1 cu.m stemtimber, kg element per acre					
	During 50 years' growth			During 100 years' growth		
	Ca	K	P	Ca	K	P
Pines	1.3	0.6	0.15	0.9	0.3	0.09
Other conifers	2.3	1.1	0.21	1.1	0.5	0.09
Hardwoods	6.2	1.7	0.38	3.8	1.0	0.23

Clearly, "hardwood" and "other conifer" thinnings remove, from their respective sites, 4 and 2 times greater quantities of nutrients respectively compared with "pine" thinnings, for the production of similar volumes of stemtimber.

(ii) *Nutrients removed from the forest-site in one rotation*

(*a*) the total quantities removed in the total thinnings up to clear-felling plus the timber of the clear-felled main-crop are shown in Table IV.

TABLE IV

Species group	Nutrients removed within the total thinnings plus main-crop by clear-felling, kg element per acre					
	After 50 years' growth			After 100 years' growth		
	Ca	K	P	Ca	K	P
Pines	98	39	9	172	67	15
Other conifers	180	88	16	363	190	30
Hardwoods	401	107	24	795	203	44

Although the nutrient-removal for two 50 year rotations is similar to one 100 year rotation, the latter yields a greater volume of stemtimber; in a longer rotation, therefore, a higher proportion of the nutrients removed go into the production of the more commercially useful timber component.

(*b*) the way in which the total quantities of nutrients removed in one rotation are distributed among the three component organs of the timber.

Table V shows the percentage distributions of nutrients among the three timber components, which for each species group are means of the several individual percentage distributions within that group.

TABLE V

Species group	Clear-felling component	Means of the percentage distributions of nutrients among the total-thinning plus clear-felling components					
		After 50 years' growth			After 100 years' growth		
		Ca	K	P	Ca	K	P
Pines	brush	50	51	61	34	37	45
	stembark	23	13	15	30	16	21
	stemwood	27	36	24	36	47	34
Other conifers	brush	58	56	63	37	36	45
	stembark	24	21	22	40	30	33
	stemwood	18	23	15	23	34	22
Hardwoods	brush	40	48	55	27	35	41
	stembark	28	17	20	51	25	27
	stemwood	32	35	25	22	50	32

The trends of the distributions are similar to those seen for the total thinnings (Table II), but the proportions in the brush have decreased, and those in the stembark and stemwood increased, corresponding to the changed composition of the clear-fellings.

Again, considerable reduction in the nutrient-removal from the site may be achieved by leaving the brush and stembark on the forest floor, but here, as with the total thinnings, such management may still leave considerable weights of nutrients, particularly Ca, immobilized in these organs on the forest floor, and unavailable to the rooting zone. Generally such management would only be justifiable upon nutrient-poor soils.

(iii) *Nutrients taken up and immobilized within all organs of the main growing crop*

(*a*) the total quantities taken up are shown in Table VI.

TABLE VI

Species crop	Total nutrients immobilized within the main growing crop, kg element per acre					
	After 50 years' growth			After 100 years' growth		
	Ca	K	P	Ca	K	P
Pines	98	57	13	115	56	12
Other conifers	208	113	25	274	152	28
Hardwoods	302	82	19	520	129	28

Clearly, considerable quantities of nutrients, particularly Ca, may be taken up and immobilized within the various organs of a growing forest; these quantities being, in the first 100 years' growth, greater than those removed from the site via the thinnings.

The relatively small increase in nutrient immobilization frequently occurring from 50 to 100 years suggests that within unexploited forests of small net annual increase in timber volume, the nutrient-immobilization may reach an upper limit, the sole nutrient-movement then being a comparatively small (see below) nutrient-cycle associated with foliar flush and fall.

The clear-felling and replanting of such a forest causes drastic nutrient-changes; a considerable nutrient-removal, particularly Ca, occurs, and a considerable new net nutrient-withdrawal from the soil commences, through the nutrient-immobilization in the newly developing tree organs. Once again, the relevance of these nutrient-demands depends upon the nutrient-supplying ability of the soil.

(*b*) the way in which the total quantities of nutrients immobilised in the main growing crop are distributed among the component organs of the main-growing crop.

Table VII shows the percentage distributions of nutrients among the five components, which for each species group are means of the several individual percentage distributions within that group.

TABLE VII

Species group	Main growing crop component	Means of the percentage distribution of nutrients among the main crop components					
		After 50 years' growth			After 100 years' growth		
		Ca	K	P	Ca	K	P
Pines	needles	23	39	43	14	28	32
	brush	25	18	21	18	14	18
	stembark	17	8	9	25	12	14
	stemwood	22	22	14	30	33	23
	roots	13	13	13	13	13	13
Other conifers	needles	26	30	40	15	17	27
	brush	30	27	25	21	20	22
	stembark	20	14	13	32	23	23
	stemwood	11	16	9	19	27	15
	roots	13	13	13	13	13	13
Hardwoods*)	leaves	11	20	22	5	10	12
	brush	22	25	28	16	21	24
	stembark	38	14	17	46	18	23
	stemwood	16	28	20	20	38	28
	roots	13	13	13	13	13	13

*) excluding those without leaves sampled in winter.

Assuming triennial needle renewal, it may be seen that for any particular nutrient, the ratios of the nutrients returned annually to the forest floor via the foliage to the nutrients immobilized annually in the woody organs (main crop plus thinnings over 100 years) are similar for all three species groups.

Species considered favourable, because of their nutrient-rich litter, therefore, may be simultaneously immobilizing within their woody organs correspondingly greater nutrient-weights, and the ultimate overall effect of the growth and removal of such species may well be greater absolute nutrient-removal from the site, rather than a more efficient circulation of nutrients within the site.

Conversely, species removing very small quantities of nutrients from the site may simultaneously produce nutrient-poor litters, incapable of supporting the more useful fauna [36] [45].

The values of the above *nutrient returned* : *nutrient removed* ratios are 3, 6 and 9 for Ca, K and P respectively, hence timber-exploited forest is particularly selective in its removal of Ca from the site.

Although these ratios show that the annual nutrient-return via the foliage is much greater than the annual nutrient-immobilization within the woody organs, the cumulative effect of the latter brings

about, relatively early in the life of the mature forest, the important characteristic that the far greater proportion *i.e.* 70–96% of the nutrients contained within the crop, are held in the woody, as distinct from foliar, organs.

The common claim that the greater part of the nutrients taken up is returned via the foliage and that negligible quantities of nutrients are removed via the timber is misleading because by implying that so long as nutrient-release is occurring in the litter, no other nutrient-demands are being made, it has focussed undue attention upon the litter, and diverted attention from the considerable cumulative nutrient-immobilization taking place in the woody organs.

From the comparison of the rates of nutrient-return and nutrient-immobilization above, it is clear that non-nutrient-release from the litter can be of considerable long term effect upon the nutrient-status of the site, but it must now be equally clear that the ultimate removal from the site via the timber of the considerable quantities of nutrients slowly accumulated and immobilized within the woody organs cannot be ignored as in the above claim, for this may be of even greater long term effect upon the nutrient-status of the site.

(iv) *The total quantities of nutrient taken up by timber-producing forest* are shown in Table VIII.

TABLE VIII

Species group	Component	Total nutrient uptake (excl. foliage and roots of thinnings and litter), kg element per acre					
		After 50 years' growth			After 100 years' growth		
		Ca	K	P	Ca	K	P
Pines	timber thinnings	35	15	4	88	35	9
	main crop	98	57	13	115	56	12
	total	133	72	17	203	91	21
Other conifers	timber thinnings	56	26	5	164	82	13
	main crop	208	113	25	274	152	28
	total	264	139	30	438	234	41
Hardwoods	timber thinnings	161	44	10	359	96	22
	main crop	302	82	19	520	129	28
	total	463	126	29	879	225	50

Clearly, these quantities of nutrients, plus any additional quantities held in the litter, represent the overall nutrient-uptakes of

timber-producing forest upon the respective sites. Again, the importance of their size can only be assessed by reference to the nutrient-supplying ability of the sites.

THE NUTRIENT DEMANDS OF FOREST COMPARED WITH AGRICULTURAL CROPS

CROP	NUTRIENT ELEMENTS AS KG. PER ACRE OF PLANTATION											
	TAKEN UP FROM THE SOIL & CONTAINED WITHIN THE TREE ORGANS OF THE MAIN GROWING CROP ON THE SITE AFTER 100 YEARS GROWTH				TAKEN UP FROM THE SOIL & REMOVED FROM THE SITE							
					CONTAINED WITHIN THE TOTAL THINNINGS OF 100 YEARS GRO.				CONTAINED WITHIN THE TOTAL THINNINGS PLUS THE MAIN CROP AFTER 100 YEARS GROWTH OR EQUIVALENT TO CLEAR FELLING AFTER 100 YEARS			
		Ca	K	P		Ca	K	P		Ca	K	P
PINES	NEEDLES	16	16	4								
	BRUSH	21	8	2	BRUSH	38	17	5	BRUSH	59	25	7
	STEMBARK	29	7	2	STEMBARK	23	5	2	STEMBARK	52	11	3
	STEMWOOD	34	18	3	STEMWOOD	27	13	2	STEMWOOD	61	31	5
	ROOTS	15	7	1								
	WHOLE TREE	115	56	12	TOTAL	88	35	9	TOTAL	172	67	15
	TOTAL DEMAND (EXCL. LITTER) ON THE SITE AT 100 YEARS									203	91	21
OTHER CONIFERS	NEEDLES	41	26	8								
	BRUSH	58	30	6	BRUSH	74	36	7	BRUSH	134	68	14
	STEMBARK	87	35	7	STEMBARK	57	21	4	STEMBARK	144	53	10
	STEMWOOD	52	41	4	STEMWOOD	33	25	2	STEMWOOD	85	59	6
	ROOTS	36	20	3								
	WHOLE TREE	274	152	28	TOTAL	164	82	13	TOTAL	363	190	30
	TOTAL DEMAND (EXCL. LITTER) ON THE SITE AT 100 YEARS									438	234	41
HARDWOODS	LEAVES	26	13	3								
	BRUSH	83	27	7	BRUSH	129	42	11	BRUSH	215	71	18
	STEMBARK	239	23	6	STEMBARK	162	17	5	STEMBARK	406	44	12
	STEMWOOD	104	49	8	STEMWOOD	68	37	6	STEMWOOD	174	88	14
	ROOTS	68	17	4								
	WHOLE TREE.	520	129	28	TOTAL	359	96	22	TOTAL	795	203	44
	TOTAL DEMAND (EXCL. LITTER) ON THE SITE AT 100 YEARS									879	225	50

AGRICULTURAL CROP

OATS: grain, 0·8 tons/acre + straw.
GRASS: hay, 1·5 tons/acre.
POTATOES: tubers, 6 tons/acre.
TURNIPS: roots, 17 tons/acre + leaf.

TOTAL NUTRIENT REMOVAL FROM THE SITE DURING 100 YEARS CROPPING OF A FOUR-COURSE ROTATION

Ca	K	P
980	3000	430

Diagram 1.

FURTHER ASPECTS OF THE ESTIMATES

(i) *Their relation to those of agriculture*

The nutrient-uptakes of forest and agricultural crops for a 100 year period are compared in Diagram 1. A fundamental difference exists; K is taken up in greatest amount by agricultural crops, but Ca in greatest amount by forest, due to mature forest being composed predominantly of woody organs which, as the composition-data in Table XI show, contain greater quantities of Ca relative to K than the foliage, which more resembles an agricultural crop.

It is interesting to note that because of this differential composition within the forest tree the nutrient demands of mature forest, and their difference from those of agriculture cannot be foretold from isolated parkland or very young trees possessing relatively high foliar: woody growth development. Thus, Schröder's 8-year old *Acer platinoides* has a K:Ca composition ratio higher than that of mature tree, whilst recent studies upon tropical forest fallow of *Musanga cecropioides* [7]) show that as the age and proportion of woody organs increase, Ca replaces K as the ion taken up in greater amount.

For all species groups the uptakes of K and P are considerably lower than those for agricultural crops, but in the case of Ca, "hardwood" forest takes up almost as much, "other conifers" one half and "pine" one fifth. Hence, the common claim that the nutrient-demands of the forest are negligible compared with those of agriculture appears to grossly underestimate the demands of the forest for Ca. But, if instead of comparing absolute uptakes, uptakes relative to the soil nutrient-status of the respective sites are considered, a truer picture of the possible effects of the nutrient-demands of the two crops upon their respective sites is obtained.

Looked at in this way, the data in Diagram 2 show that nutrient-demands of forest and *Calluna* relative to the soil nutrient-status of their sites are all greater than the nutrient-demands agricultural crops make upon agricultural soils, and particularly more nutrient-demanding is pine or birch compared with *Calluna* on almost the same moor soil.

Thus, although afforestation of nutrient-poor moor soils appears, at first sight, to increase site-productivity considerably compared

THE NUTRIENT DEMANDS OF THE CROP COMPARED WITH THE NUTRIENT CONTENTS OF THE SOIL FOR AGRICULTURAL, HIGHLY PRODUCTIVE FOREST, 'NATURAL' CALLUNA AND AFFORESTED CALLUNA MOOR SOILS.

CROP	STEM TIMBER + BRUSH YIELD & CROP WEIGHTS PER ACRE	pH 1:5 H_2O	NUTRIENT ELEMENTS AS KG. PER ACRE						
			CALCIUM		POTASSIUM		PHOSPHORUS		NITROGEN
			TOTAL	AVAIL.	TOTAL	AVAIL.	TOTAL	AVAIL.	TOTAL
AGRICULTURE (EBBERSTON)									
PLANT (ONE ANNUAL CROP)			10		30		4		29
SOIL TOP 25 CM		5·4		1163		11	533	28	2065
SOIL TOP 50 CM		5·8		2206		24	1268	45	2885
RATIO PLANT: TOP 50 CM AVAIL. SOIL NUTRIENT			·0045		1·25		·096		·01*
QU.CL.I SITKA SPRUCE (THORNTON DALE)									
PLANT GROWING AT 70 YEARS			240		130		27		
PLANT REMOVED IN 70 "			110		39		10		
SOIL TOP 25 CM		5·1	2080	1401		11	307	28	1954
SOIL TOP 50 CM		6·4		3824		31	587	53	2583
RATIO PLANT: TOP 50 CM AVAIL. SOIL NUTRIENT			·092		5·5		·70		
QU.CL.I SCOTS PINE (SCAMPSTON)									
PLANT GROWING AT 150 YEARS			130		56		12		250
PLANT REMOVED IN 150 "			100		33		7		160
SOIL TOP 25 CM		5·2	671	398		13	592	48	1294
SOIL TOP 50 CM		4·8	1496	676		22	1158	89	2264
RATIO PLANT: TOP 50 CM AVAIL. SOIL NUTRIENT			·34		4·0		·21		·18*
CALLUNA MOOR (SILPHO)									
PLANT	5,000 KG.		9		9		2		40
LITTER	1,700 KG	3·3	2		1		1		17
SOIL PROFILE: CM. 0–3 RAW HUMUS		3·1	41	17		9	32	9	660
3–28 BLEACHED		3·9	196	10		8	117	10	694
28 PAN		4·2	4				7		9
28–50 SUBSOIL		4·5	321	9		15	250	4	199
SOIL ABOVE THE PAN			237	27		17	149	19	1354
SOIL TOP 50 CM			562	36		32	406	23	1562
RATIO PLANT+LITTER: TOP 50 CM AVAIL. SOIL NUTRIENT			·29		·31		·14		·036*
PINE AFFORESTED MOOR (SUFFIELD)									
PLANT GROWING AT 80 YEARS	141 CU.M.		108		56		12		200
PLANT REMOVED IN 80 "	45 CU.M.		67		27		6		100
LITTER	14,900 KG.	3·1	27		10		10		190
SOIL PROFILE: CM. 0–8 RAW HUMUS		2·9	161	32		8	30	9	856
8–30 BLEACHED		3·6	440	42		17	112	15	720
30 PAN		4·3	6				8		4
30–50 SUBSOIL		4·5	230	9		13	112	6	119
SOIL ABOVE THE PAN			601	74		26	141	24	1576
SOIL TOP 50 CM			837	83		39	261	30	1699
RATIO PLANT+LITTER: TOP 50 CM AVAIL. SOIL NUTRIENT			2·4		2·4		·95		·29*
BIRCH AFFORESTED MOOR (SUFFIELD)									
PLANT GROWING AT 60 YEARS	66 CU.M.		38		28		8		} (134)
PLANT REMOVED IN 60 "	45 CU.M.		20		12		5		
LITTER	6,100 KG.	3·2	21		5		6		106
SOIL PROFILE: CM. 0–6 RAW HUMUS		3·2	141	71		5	28	7	708
6–29 BLEACHED		3·7	435	38		6	195	27	873
29 PAN									
29–50 SUBSOIL		4·4	185	6		4	216	10	195
SOIL ABOVE THE PAN			576	109		11	223	34	1581
SOIL TOP 50 CM			761	115		15	439	44	1776
RATIO PLANT+LITTER: TOP 50 CM AVAIL. SOIL NUTRIENT			·69		3·0		·42		(·14)*

NOTE: THE NUTRIENT DEMANDS OF THE AGRICULTURAL CROP ARE BY R. WARINGTON; THOSE FOR TREES FROM P.J. RENNIE'S SUMMARY OF THE LITERATURE. ALL SITE, SOIL, LITTER AND PLANT DATA ARE FROM RENNIE'S YORKSHIRE STUDIES. 'AVAIL.' Ca & K = EXCHANG.; 'AVAIL.' P EXTR. BY 8-HYDROXYQU. IN ACET. AC. * RATIO TOTAL : TOTAL NITROGEN.

Diagram 2.

with former pastoral uses, the serious question posed is for how long are such soils able to fulfil these greatly increased nutrient demands, for until the forester knows this, he cannot be certain that the maximum site-productivity (at the existing soil nutrient-status) is not, in reality, the apparently primitive pastoral use, and that his greater productivity is destined to be ephemeral by reason of the rapid nutrient-depletion it causes.

(ii) *The reproducability of the estimates*

Although the mean estimates are based on a wide range of common species upon several soil types, it is important to know how often similar forest growth elsewhere would show estimates of the same order, and the conditions under which the uptakes may differ appreciably from these values; the variation among the individual estimates provides some information upon these aspects; Table IX shows the individual overall uptakes over the 100-year growth period, their Means, and Fiducial Limits at $P = .20$.

Estimates appreciably below the lower fiducial limit are marked "B", those appreciably above the upper limit, "A".

From the analysis, the probability is that four times out of five mean estimates based on similar material would give values lying within the fiducial limit values shown, and nine times out of ten they would not be lower than the lower fiducial limit values. Hence, although a certain amount of fluctuation in the mean estimates is to be expected, the size of this fluctuation is too small to invalidate the general conclusions reached earlier, based on the mean estimates.

The conclusions, therefore, and mean estimates with the ranges shown, are of very wide application. But exceptions to the general are possible; further examination of the individual estimates below provides some evidence of how they arise and when they may be important.

(iii) *Nutrient uptake and quality class*

Table IX shows, with a minority of exceptions, that within each group of species forest growth making the smaller overall nutrient-demands is of a lower or poorer quality class; and conversely, greater timber production is unavoidably accompanied by a greater nutrient-demand upon the site.

The unique comparison by W i l l, shown in Table X, of similar

TABLE IX

Species, quality class or species group	Individual, mean and fiducial limits of mean, estimate of total nutrient demand upon the sites at 100 years, kg element per acre		
	Ca	K	P
P. silvestris I	299	76	23
P. silvestris II	210	112	20
P. silvestris V	133	66	13
P. strobus II	166	110	25
means	203	91	21
"Pines" fiducial limits	143 261	72 110	16 25
A. alba I	377	281	50
A. alba II	760 A	432 A	61
A. alba IV	112 B	285	50
P. excelsa I	514	208	33
P. excelsa II	738 A	194	43
P. excelsa IV	292	151	34
L. decidua III	269	87 B	19 B
means	438	234	41
"Other conifers" fiducial limits	304 570	173 295	32 51
Betula alba II	88 B	64 B	18 B
Fagus sylvatica I	371 B	259	49
,, ,, III	328 B	272	46
,, ,, IV	331 B	166	18 B
,, ,, I	1011	179	32
,, ,, I	707	308	40
Quercus robur I	1348 A	431 A	120 A
,, ,, I	1448 A	347 A	95 A
,, ,, III	267 B	154 B	16 B
,, ,, I	1958	266	60
Carpinus betulus I	1260	271	85 A
,, ,, II	1842 A	92 B	47
Alnus glutinosa III	252 B	55 B	20 B
Fraxinus excelsior I	539 B	283	47
,, ,, II	667	172	53
Populus tremula III	612	91 B	19 B
Robinia pseudoacacia II	1895 A	418 A	75 A
means	879	225	50
"Hardwoods" ficucial limits	674 1082	188 263	41 60

aged, Quality Class I and V *Pinus silvestris*, illustrates in greater detail, how this difference in nutrient-demand comes about.

For all four nutrients the differences between overall uptakes are made up more by differences in nutrient-removal via the thinnings and less by differences in nutrient-immobilization within the main growing crops; suggesting that poorer quality-class growth generally

TABLE X

Quality class	Nutrient element			
	Ca	K	P	N
	Nutrient uptake (g) per whole stembark of one tree			
I	366	42	18	228
V	200	28	8	142
ratio	1.83	1.50	2.25	1.61
	Nutrient uptake (g) per whole needles of one tree			
I	81	68	22	256
V	51	62	12	122
ratio	1.59	1.10	1.83	2.10
	Nutrient uptake (g) per whole organs of one tree			
I	1373	398	119	2663
V	752	305	57	1443
ratio	1.83	1.31	2.09	1.85
	Nutrient removal (kg/acre) via the thinnings of 100 years' growth			
I	133	32	10	158
V	38	10	2	60
ratio	3.50	3.20	5.00	2.64
	Nutrient immobilization (kg/acre) in the main growing crop at 100 years			
I	166	44	13	230
V	95	56	11	162
ratio	1.75	0.79	1.18	1.42
	Total nutrient demand (kg/acre) upon the site at 100 years			
I	299	76	23	388
V	133	66	13	222
ratio	2.25	1.15	1.77	1.75

may be more disadvantageous to the forester because the reduction in timber thinnings obtained is much greater proportionately than the reduction in overall-nutrient-uptake from the site.

Table X shows a further important point; relative differences between quality-classes of both nutrient-uptake per tree, and overall nutrient-uptake per acre, do not correspond with, and hence cannot be forecast from, relative differences in foliar-uptake; the more striking weakness of foliar-analysis here being the underestimation of Ca, and overestimation of N, overall-uptake differences.

As foliar-analysis has been shown to be incapable of reflecting true differences in nutrient-uptake arising from growth differences for varied types of tree species [2] [13], the use of an alternative organ, may sometimes prove more reliable for this purpose; the data in Table X suggest that for Ca and N, but not K, the stembark may be more able to do this.

(iv) *Variation in uptake among different species*

Table IX shows that, with the exception of a few anomalies, the classification of the individual overall-uptakes into the three broad groups "pines", "other conifers" and "hardwoods" is justifiable, but the data upon different species of similar quality class are so few that much more work is necessary to confirm some of the interesting differences suggested.

Thus, *Quercus robur*, Q.C. I, whether upon soil derived from Bunter sandstone or calcareous oolite, shows overall-uptakes of all three nutrients greatly in excess of the average "hardwood" values; *Carpinus betulus* Q.C. I and II upon oolite and granite respectively take up greater than average amounts of Ca, whilst *Robinia pseudo-acacia* Q.C. II on diluvial sand takes up excessive amounts of all three nutrients. *Abies alba* and *Picea excelsa*, both Q.C. II upon diluvial sand take up excessive amounts of Ca, and the former species excessive amounts of K and P. In all cases these excessively high uptakes are due primarily to the greater nutrient-uptakes by the timber organs.

Neither *Fraxinus excelsior* Q.C. I upon diluvial sand nor *F. excelsior* Q.C. II upon oolite make demands differing appreciably from the average.

Very appreciably lower than average amounts of all three nutrients, but especially Ca, are taken up by *Betula alba* Q.C. II upon a quartz rich schist, due partly to the smaller yield of timber and partly to the smaller nutrient concentration within the stembark (Table XI); but the only corroboration of these uniquely low values is seen in a partial analysis of a specimen in another country, also by Schröder.

Fagus sylvatica Q.C. I upon both Bunter sandstone (the same forest as *Q. robur* above) and tertiary sandstone with morainic material take up exceptionally small amounts of Ca, but rather larger than average amounts of K, the small Ca-uptake being due to the small Ca-uptake and concentration in the stembark.

Of the several species upon oolite compared by Henry *Prunus avium* is notable for its exceptionally low uptake of all three nutrients, again due primarily to lower stembark uptake.

Thus within each species group, different species upon the same soil and of similar quality-class, appear to make different nutrient-demands upon the site. Clearly such variation may be of considerable

pedological and silvicultural importance, particularly upon nutrient-poor soils. Before implementing any large-scale afforestation scheme upon nutrient-poor soils, therefore, it would appear to be of some considerable importance to know the approximate nutrient-demands of the various possible species, upon the various soils making up the area.

(v) *Variation in uptake within the same species*

Table IX shows that variation in overall-uptake can occur within the same species of the same quality-class. But comparative data for such species are very few, and with one exception, always concern species upon different soils and have the disadvantage of necessitating the comparison of estimates based upon different authors' experimentation.

Overall-uptakes based on two unequal aged specimens of *Q. robur*, both Q.C. I, and sampled from the same forest by Weber showed good agreement.

All other comparisons viz., *F. sylvatica* I and I upon Bunter and oolite; *Q. robur* I and I upon Bunter and oolite; *C. betulus* I and II upon diluvial sand and oolite; and *F. excelsior* I and II upon diluvial sand and oolite show a greater relative Ca- and lower relative K-uptake, and except in one instance, a lower relative P-uptake upon the oolitic site.

For *F. sylvatica* and *C. betulus* the relative fluctuations in K, and especially Ca uptake, are greater than for *Q. robur* and *F. excelsior*.

A. alba I and II upon Granite and Diluvial Sand and *P. excelsa* I and II upon these same two formations show appreciably greater Ca, but no decreased K-uptake, upon the diluvial sand.

The higher quality class pines show relatively little variation in the uptake of any nutrient, but the known variable composition of *P. maritima* upon different soils [24]) [25]) suggests that greater variation for pines may be possible.

The nutrient-uptakes of the same tree species may fluctuate, therefore, solely through soil differences, and the extent of this fluctuation may differ appreciably for different species.

Because the uptakes of different nutrients do not necessarily fluctuate in the same direction, the uptake of these three nutrients need not be all maximal or all minimal upon any particular site.

Clearly, much research is needed to elucidate the minimum

TABL

A summary of the original composition and weigh

Note: All nutrients are expressed as elemental weight

A

	Species	Author	Year	Ref. No.	Age of tree (years)	Quality class	Origina Time of sampling
1	*Pinus silvestris*	Will	1882	80	100	I, Schwappach	May
2	*Pinus silvestris*	Ramann	1881	50	100	II, Schwappach	August
3	*Pinus silvestris*	Will	1882	80	100	V, Schwappach	April
4	*Pinus strobus*	Ramann *et al.*	1882	53	50	(II, Schwappach)	October
5	*Pinus strobus*	Weber	1893	77	66	(II, Schwappach)	
6	*Abies alba*	Weber	1881	76	144	I, Schwappach	Autumn
7	*Abies alba*	Councler	1886	16	40	II, Schwappach	May
8	*Abies alba*	Schröder	1878	64	90	IV, Schwappach	April
9	*Picea excelsa*	Weber	1881	76	120	I, Schwappach	Autumn
10	*Picea excelsa*	Councler	1886	16	40	II, Schwappach	May
11	*Picea excelsa*	Schröder	1874	63	100	IV, Schwappach	May
12	*Larix decidua*	Councler	1886	16	40	III, Wiedemann	May
13	*Larix decidua*	Weber	1893	77	80	I, Wiedemann	
14	*Larix decidua*	Weber	1893	77	45	I, Wiedemann	
15	*Betula alba*	Schröder	1878	64	50	II, Schwappach	February
16	*Betula alba*	Schröder	1865	62	*ca* 85	II, Schwappach	August
17	*Fagus sylvatica*	Weber	1876	75	50	I, Schwappach	March
18	*Fagus sylvatica*	Weber	1876	75	90	III, Schwappach	March
19	*Fagus sylvatica*	Weber	1876	75	220	IV, Schwappach	March
20	*Fagus sylvatica*	Heyer *et al.*	1852	27	*ca* 75	II, Schwappach	January
21	*Fagus sylvatica*	Henry	1878	26	37	I, Schwappach	June
22	*Fagus sylvatica*	Gaumann	1935	22	110	I, Schwappach	January
23	*Quercus robur*	Weber	1876	75	25	I, Schwappach	March
24	*Quercus robur*	Weber	1876	75	50	I, Schwappach	March
25	*Quercus robur*	Weber	1876	75	345	III, Schwappach	March
26	*Quercus robur*	Henry	1878	26	37	I, Schwappach	June
27	*Carpinus betulus*	Ramann *et al.*	1882	54	40	(I, Schwappach)	Septembe
28	*Carpinus betulus*	Henry	1878	26	37	(II, Schwappach)	June
29	*Carpinus betulus*	Weber	1893	77	82	(III, Schwappach)	
30	*Alnus glutinosa*	Ramann *et al.*	1882	52	70	III, Schwappach	Septembe
31	*Fraxinus excelsior*	Ramann *et al.*	1883	55	40	I, Wiedemann	Septembe
32	*Fraxinus excelsior*	Henry	1878	26	37	II, Wiedemann	June
33	*Populus tremula*	Weber	1893	77	40	III, Tjurin	
34	*Populus tremula*	Henry	1878	26	37	III, Tjurin	June
35	*Robinia pseudo-acacia.*	Ramann	1883	51	30	II, Erteld	October
36	*Corylus avenalla*	Henry	1878	26	37		June
37	*Sorbus terminalis*	Henry	1878	26	37		June
38	*Acer campestre*	Henry	1878	26	37		June
39	*Ulmus montana*	Henry	1878	26	37		June
40	*Prunus avium*	Henry	1878	26	37		June
41	*Malus acerba*	Henry	1878	26	37		June
42	*Acer platinoides*	Schröder	1878	64	8		May

n.d. = not determined

*) stemwood plus stembark

a, and the evaluated nutrient uptake estimates.
ar-felling nutrient-removals include the thinnings to date.

a

Site and soil	Oven dry weight (kg) of the whole of each organ of the one sample tree					
	Roots	Stem-wood	Stem-bark	Brush	Needles or Leaves	
	127	614	49	92	17	1
berswalde; diluvial sand, podzolic from description.	n.d.	597	39	55	26	2
	95	298	35	86	11	3
berswalde; diluvial sand.	n.d.	70	10	21	5.5	4
Viesen, Spessart: derived from Bunter sandstone.						5
ohenhau Revier, Bavaria: derived from granite.	n.d.	1059	202	131	38	6
feil's forest, Eberswalde: derived from diluvial sand.	9	34	7	13	9	7
harandt; schist.	n.d.	109	15	14	14	8
ohenhau Revier ,Bavaria: derived from granite.	n.d.	897	85	115	29	9
feil's forest, Eberswalde: derived from diluvial sand.	12	42	6	20	11	10
harandt, quartz rich schist.	n.d.	308	42	51	22	11
feil's forest, Eberswalde: derived from diluvial sand.	19	50	6	11	0.9	12
othenbuch, Hochspessart: derived from Bunter sandstone.	n.d.	1330	154	n.d.	n.d.	13
ochberg, Guttenberg: derived from Muschelkalk.	n.d.	214	n.d.	n.d.	n.d.	14
harander Revier; quartz rich schist.	n.d.	74	16	23		15
orpat (Lithuania).						16
othenbuch Revier, Hochspessart: soil said to be the same as under the oak (see below).	n.d.	67	3.5	39		17
	n.d.	226	17	57		18
	n.d.	1037	69	116		19
esse (?); basalt-derived soil.						20
rande-Haye, Nancy; (see below).	n.d.	29	2	8.6	2	21
rich, Tertiary sandstone plus moraine.	150	1400	75	300		22
othenbuch Revier, Hochspessart: derived from Bunter sandstone, 4 cm litter, 3 cm humus, 10 cm	n.d.	5	1	1.6		23
	n.d.	93	13	31		24
humus soil, 60–80 cm rooting zone with weathered parent material below.	n.d.	1845	120	713		25
rande-Haye, Nancy; (see below).	n.d.	29	4.5	8.5	2.4	26
berswalde: podzolic, diluvial sand.	n.d.	71	6	31	3.3	27
rande-Haye, Nancy; (see below).	n.d.	22	1.5	10.5	3	28
chaffenburg: derived from granite.	n.d.	264*		n.d.	n.d.	29
berswalde: podzolic from description, diluvial sand.	n.d.	213	45	18	2.8	30
berswalde.	n.d.	60	6	37	6	31
rande-Haye Nancy: (see below).	n.d.	32	3	11	3.8	32
othenbuch, Spessart: derived from Bunter sandstone						33
rande-Haye, Nancy: (see below).	n.d.	16	5.2	6.6	1.5	34
berswalde, podzolic, diluvial sand.	n.d.	125	25	21	4.5	35
rande-Haye, Nancy: a clayey soil derived from Lower Oolite, free from glacial sand, and containing no free $CaCO_3$. 0–15 cm clayey soil; 15–20 cm calcareous stones with soil between; 20 + cm fissured calcareous material.	n.d.	6.1	1.8	6.6	1.5	36
	n.d.	31	4	12	2	37
	n.d.	29	3.8	12	3.6	38
	n.d.	16	2.3	6.3	1.1	39
	n.d.	11	1.8	6.7	0.4	40
	n.d.	16	2.3	8.8	2.2	41
harandt.	n.d.	.87	.12	.18	.13	42

TABL

B

	Original data														
	Total weight (g) of each nutrient contained in each whole organ of the one sample tree														
	Roots			Stemwood			Stembark			Brush			Needles or Leaves		
	Ca	K	P	Ca	K	P	Ca	K	P	Ca	K	P	Ca	K	P
1	141	66	17	525	135	35	366	42	18	260	87	27	81	68	22
2				402	203	29	212	40	5.2	137	81	17	92	124	26
3	82	49	8.5	192	88	12	200	28	8	228	78	16	51	62	12
4				32	36	3.8	44	25	6	67	31	11	18	11	4
5															
6				562	449	39	664	604	106	229	88	34	189	176	39
7				20	23	2.5	58	28	3.9	56	31	3.1	102	32	11
8	17	11	2	22	94	6.7	28	46	8.7	17	45	10	33	51	17
9				529	339	49	948	191	30	244	107	16	114	136	37
10				39	11	1.8	82	17	3	134	34	10	95	44	12
11	28	10	2	148	89	6	214	40	11	125	74	15	69	71	33
12				32	14	2.0	62	16	3.9	65	17	4.3	4	12	2
13	60	14	3.2	730	380	94	577	327	259						
14															
15				35	34	7	36	13	4	35	30	12			
16															
17				47	69	10	66	5	1.5	101	82	21			
18				199	319	25	235	29	27	147	137	33			
19				1160	813	94	1590	295	36	303	275	26			
20															
21				45	12	1.3	67	5	1	65	14	3.7	34	20	2
22				1175	1086	100	1900	362	49.2	1354	508	91			
23	622	243	35	3.6	5.2	1.4	23	2.7	0.5	8.5	3.4	1.3			
24				70	90	16	610	32	16	153	71	21			
25				703	1604	61	2443	180	98	1703	1023	124			
26				50	7.3	1.4	158	6.3	3.2	102	25	4.2	37	21	6
27				58	51	6.6	297	22	14	193	46	16	30	17	8
28				43	3.3	1.4	81	2.4	.1	99	7.6	5.6	69	15.8	6
29				862*	235*	49*									
30				128	92	39	734	60	26	163	42	13.1	35	22	4
31				42	67	8.4	124	20	2.4	178	105	27	154	48	8
32				51	13	3.2	76	9	2.3	90	29	7.1	76	42	27
33															
34				33	6.3	1.2	91	11.2	2.4	85	11.3	2.1	48	21	5
35				339	65	10.1	678	149	20	197	57	18	230	13.3	3
36				14	1.9	0.6	99	2.2	2.2	68	8	3.1	36	15	3
37				51	4.4	1.8	132	11.2	2.3	135	20.8	4.5	39	26	3
38				49	7	1.4	190	11.4	4.7	95	12	3.9	37	36	7
39				40	3.7	1	128	4.7	1.4	76	9.4	2.9	16	15	2
40				17	1.5	0.8	23	1.3	0.5	47	6.7	1.5	9	6	0
41				29	3.7	0.7	115	5.8	1.5	137	11	3.5	66	35	5
42				.8	.4	.16	3.8	.5	.17	1.8	.5	.14	1.7	.3	1

*) stemwood plus stembark **) excluding bark †) brush yields reckoned as 0.2 of stem tim

continued)

Evaluated data										
ume (cu.m) of one sample tree		Volume (cu.m) yield of one acre of even-aged pure plantation of the various species								
		After 50 years' growth				After 100 years' growth				
		Main crop		Total thinnings		Main crop		Total thinnings		
em-ber	Brush	Stem-timber	Brush	Stem-timber	Brush	Stem-timber	Brush	Stem-timber	Brush	
0	.216	114	21	43	20	173	17	142	34	1
6	.139	92	21	31	25	145	16	114	40	2
0	.185	25	19	3.6	5.3	66	16	40	13	3
5	.058	(92)	(21)	(31)	(25)	(145)	(16)	(114)	(40)	4
										5
	.26	171	49	51	28	390	55	219	45	6
55	.0311	124	42	27	30	316	48	164	48	7
0	.0296	42	35	1.2	15	190	33	83	38	8
	.21	166	35	40	29	297	37	242	69	9
7	.0484	120	37	24	29	245	31	183	55	10
6	.0895	52	36	4	26	146	25	93	59	11
8	.0272	76	25	23	20	122	25	72	12	12
		128		62		206		136		13
2**)		115**)		56**)		185**)		122**)		14
5	.0454	48	12	22	4.5	63	15	73	16	15
		48		22		63		73		16
1	.065	94	24	28	12	208	27	113	26	17
4	.098	48	20	4.5	2	140	24	75	17	18
9	.196	24	23	0.4	0.8	104	21	55	17	19
										20
36	.0146	94	24	28	12	208	27	113	26	21
	.28	94	24	28	12	208	27	113	26	22
9	.0023	72	12	53	47	161	18	164	61	23
8	.0413	72	12	53	47	161	18	164	61	24
6	.991	22	17	15	16	92	13	97	44	25
9	.0118	72	12	53	47	161	18	164	61	26
3	.0489	(94)	(24)	(28)	(12)	(208)	(27)	(113)	(26)	27
31	.0148	(70)	(22)	(13)	(6)	(176)	(26)	(93)	(24)	28
										29
0	.035	52	8.5	17	6.5	63	7.3	31	9	30
3	.066	108	18	24	23	172	17	62	33	31
52	.0199	66	19	12	24	130	17	38	36	32
		81	9	27	3					33
64	.0144	81	9	27	3	118	13	41	4	34
15	.0310	108	20 †)	84	15 †)	140	25 †)	113	21 †)	35
										36
										37
										38
										39
										40
										41
										42

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	Nutrients (kg) removed from one acre of forest site in 50 years											
	Total thinnings						Clear-felling					
	Stem timber			Brush			Stem timber			Brush		
	Ca	K	P	Ca	K	P	Ca	K	P	Ca	K	
1	28	6	1.6	24	8	2.5	102	21	6	49	16	
2	15	6	0.8	25	15	3.1	59	24	3.3	46	27	
3	2	0.6	0.1	7	2.3	0.5	16	5	0.8	30	10	
4	10	8	1.3	29	13	4.7	40	32	5.1	53	24	
5	4	4	0.7				15	15	2.7			
	13	5	1	22	10	3	49	19	4	49	20	
6	19	16	2.2	25	10	3.7	83	71	9.8	68	27	1
7	22	14	1.8	54	30	3	124	80	10	130	72	
8	0.2	0.5	0.2	9	23	5.1	7	20	2.2	29	76	1
9	25	9	1.4	34	15	2.2	130	47	7	75	33	
10	21	5	0.8	80	20	6.0	127	29	4.7	183	46	1
11	2.2	0.8	0.1	36	21	4.4	30	11	1.4	86	51	1
12	18	6	1.2	48	13	3.2	79	25	5	108	29	7
13	31	17	9				95	52	25			
14	16**)	9**)	2**)				48**)	27**)	6**)			
	14	7	1	42	19	4	76	39	6	104	49	1
15	9	6	1.5	3	3	1.1	30	20	4.7	12	11	
16	11	4	1.7				35	12	5.4			
17	22	15	2.4	19	15	3.9	97	64	10	56	45	1
18	5	4	0.6	3	3	0.7	57	46	6.9	33	31	
19	0.6	0.2	0.1	1.2	0.5	0.1	38	15	1.7	36	32	
20	15	6	1.7	13	4	2	96	37	11	62	21	
21	58	9	1.2	53	11	3	254	39	5.2	159	34	
22	34	16	1.6	58	22	3.9	151	71	7.3	173	65	1
23	160	47	11	173	69	26	376	111	26	217	87	3
24	173	31	8	174	81	24	408	73	19	218	102	3
25	12	7	0.6	28	16	2	30	17	1.5	57	34	
26	187	13	4.1	405	100	17	441	30	10	509	126	2
27	81	17	5	48	11	4	352	73	19	143	34	1
28	49	2	0.9	40	3	2.3	313	15	6	188	14	1
29	12	3	0.7				138	37	8			
30	27	5	1.9	30	8	2.4	108	19	8	70	18	
31	32	17	2.1	62	37	9.3	178	93	11.6	111	66	1
32	23	4	1	109	35	9	151	26	7	195	63	1
33	17	23	1.1				68	93	4.4			
34	73	11	2.1	18	2	0.4	289	42	8.4	71	9	
35	470	99	14	95	28	8.7	1075	226	32	222	65	2
	80	20	4	81	24	6	241	56	11	130	51	1
36												
37												
38												
39												
40												
41												
42												

**) excluding bark

(continued)

Nutrients (kg) contained within the tree organs of one acre of growing forest after 50 years' growth										
Stem timber		Brush			Needles or Leaves			Whole Tree		
K	P	Ca	K	P	Ca	K	P	Ca	K	P	
15	4.4	25	8	2.6	17	14	4.5	134	43	13	1
18	2.5	21	12	2.6	22	31	6.5	100	70	13	2
4	0.7	23	8	1.6	38	46	9	86	67	13	3
24	3.8	24	11	4	10	6	2.4	73	47	12	4
11	2										5
17	3	24	10	3	22	22	5	98	57	13	
55	8	43	17	6.4	40	37	8.2	160	126	26	6
66	8.3	76	42	4.2	186	58	20	420	191	37	7
19	2	20	53	11.8	26	39	13	61	128	31	8
38	6	41	18	2.7	20	24	7	191	92	16	9
24	4	103	26	7.6	99	46	13	355	110	27	10
10	1.3	50	30	6	35	36	17	130	87	28	11
19	3.8	60	16	4	2	6	1.4	142	47	11	12
35	17										13
*) 18**)	4**)										14
34	5	62	31	7	54	33	10	208	113	25	
14	3.2	9	8	3.1				35	25	7	15
8	3.7										16
49	8	37	30	8				128	91	20	17
42	6.3	30	28	6.7				94	81	15	18
15	1.7	35	32	3				83	54	5	19
31	9.3	49	17	8							20
30	4	106	23	6	27	16	2.2	379	79	14	21
55	5.7	115	43	7.7				266	113	15	22
64	15	44	18	7				300	94	25	23
42	11	44	21	6				320	73	20	24
10	0.9	29	18	2.1				54	32	3.5	25
17	5.6	104	26	4.3	25	14	4.1	440	66	16	26
56	16	95	23	8	23	12	6.8	446	105	36	27
13	5.1	148	11	8.4	69	16	6.1	550	46	23	28
34	7										29
14	6.1	40	10	3.2	11	7	1.3	152	36	12	30
76	9.5	49	29	7.3	62	19	3.5	295	142	23	31
22	5.6	86	28	6.8	66	37	23	321	100	41	32
70	3.3										33
31	6.3	53	7.1	1.3	31	14	3.2	350	60	12	34
127	18	127	37	11.6	59	3	1	910	192	36	35
34	7	67	21	5	33	16	4	302	82	19	
3	2.2	54	6	2.5	29	12	2.6	200	24	8	36
12	3.3	108	17	3.6	31	21	3.1	328	47	11	37
15	4.9	76	10	3.1	30	29	5.7	341	62	16	38
7	1.9	61	7	2.3	13	12	2.1	240	30	7	39
2	1	38	5	1.2	7	5	0.6	89	14	3	40
8	1.8	110	9	2.8	53	28	4.1	320	52	10	41
								253	38	9	
									4.5	2	42

TAB

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	Nutrients (kg) removed from one acre of forest site in 100 years											
	Total thinnings						Clear-felling					
	Stem timber			Brush			Stem timber			Brush		
	Ca	K	P	Ca	K	P	Ca	K	P	Ca	K	P
1	92	18	5.5	41	14	4.3	204	40	12	62	21	6
2	55	22	3	39	23	4.9	125	50	6.9	55	32	6
3	22	4	1.1	16	5.5	1.1	59	15	3	36	12	2
4	37	30	4.8	46	21	8	84	68	11	64	30	11
5	13	14	2.5				30	31	6			
	50	18	4	38	17	5	113	42	8	59	25	7
6	82	70	10	40	15	6	228	196	27	89	34	13
7	134	89	11	86	48	5	393	258	32	172	96	10
8	13	38	4	22	58	13	44	124	13	41	110	24
9	154	55	8	80	35	5	342	123	18	123	54	8
10	162	37	6	153	39	11	378	87	14	239	61	18
11	51	18	2.4	83	49	10	130	46	6	118	70	14
12	57	18	3.6	29	8	1.9	154	49	9.7	89	24	6
13	68	37	18				172	93	46			
14	34**)	20	4**)				85**)	50**)	11**)			
	90	46	6	74	36	7	229	112	16	134	68	14
15	31	21	5	12	11	4.1	58	39	9	24	21	8
16	37	12	5.7				68	22	11			
17	91	60	10	40	33	8.4	258	170	28	82	67	17
18	83	66	10	26	24	5.7	237	190	28	62	58	14
19	85	34	4	26	24	2.2	245	99	11	58	53	5
20	106	41	12	54	18	8.3	306	118	35	111	38	17
21	235	36	4.8	116	25	6.6	670	102	14	236	51	13
22	138	65	6.7	126	47	8.5	393	185	19	256	96	17
23	493	146	35	225	90	34	977	289	69	291	117	44
24	537	96	25	226	105	31	1065	190	50	293	136	40
25	80	45	4	75	45	5.5	155	88	8	97	58	7
26	579	39	13	529	129	22	1147	77	25	685	167	28
27	326	67	19	103	24	9	927	191	55	210	49	18
28	350	17	7	162	12	9	1290	49	20	334	25	19
29	197	53	11				554	153	32			
30	48	8	3.6	42	11	3.4	147	25	11.1	76	20	6
31	84	44	5.5	89	53	13.4	316	166	21	135	80	20
32	74	13	3.2	163	52	13	325	57	14	240	77	19
33	26	36	1.7				101	140	6.5			
34	110	16	3.2	27	3.5	0.7	425	62	12	104	10	2
35	632	134	19	133	39	12.2	1415	299	42	292	85	27
	230	54	11	129	42	11	580	132	26	215	71	18
36												
37												
38	These uptake estimates represent 37 years' growth assuming 800 stems per acre.											
39												
40												
41												
42	This uptake estimate represents 8 years' growth assuming 1,000 stems per acre.											

**) excluding bark

ntinued)

utrients (kg) contained within the tree organs of one acre of growing forest after 100 years' growth

Stem timber		Brush			Needles or Leaves			Whole tree			
	K	P	Ca	K	P	Ca	K	P	Ca	K	P	
	22	6.6	21	7	2.1	11	9	3	166	44	13	1
	28	3.9	16	9	2	15	21	4.3	116	67	12	2
	11	1.9	20	7	1.4	25	31	6	95	56	11	3
	38	6	18	9	3	7	4	1.6	83	59	12	4
	17	3.2										
	25	5	21	8	2	16	16	4	115	56	12	5
	126	17	49	19	7	27	25	5.5	255	196	34	6
	169	21	86	48	5	124	39	13	540	295	45	7
	86	9	19	52	11	17	26	9	77	189	33	8
	68	10.1	43	19	2.8	13	16	4.3	280	118	20	9
	50	8	86	22	6.4	66	30	8.3	423	118	26	10
	28	3.7	35	21	4.2	23	24	11	158	84	22	11
	31	6.1	60	16	4	2	6	1.4	183	61	13	12
	56	28										13
*)	30**)	7**)										
	76	11	58	30	6	41	26	8	274	152	28	14
	18	4.2	12	10	3.8				45	32	9	15
	10	5										16
	110	18	42	34	8.7				240	166	31	17
	124	18	36	34	8.1				219	182	30	18
	65	7	32	29	2.7				220	108	12	19
	77	23	57	20	9							20
	66	9	120	26	7	18	10	1.4	660	118	20	21
	120	12.4	130	49	8.7				443	194	24	22
	143	34	66	27	10				630	195	51	23
	94	25	67	31	9				685	146	39	24
	43	4	22	13	1.6				112	64	6	25
	38	13	156	38	6.4	16	9	2.7	850	98	25	26
	124	36	107	25	9	15	8	4.5	831	180	57	27
	32	13	174	13	10	45	10	4	1330	63	31	28
	100	21										29
	17	7.5	34	9	2.7	7	5	0.9	162	36	13	30
	122	15	46	27	7	41	13	2.3	366	186	28	31
	44	11	77	25	6.1	44	24	15	430	107	37	32
	104	4.8										33
	46	9.1	77	6	1.9	20	9	2.2	475	71	15	34
	165	23	159	46	15	39	2.2	0.6	1130	245	44	35
	72	14	83	27	7	26	13	3	520	129	28	
												36
												37
												38
												39
												40
												41
												42

nutrient-uptakes necessary for timber production, as distinct from "luxury" uptakes which may be sometimes measured.

THE NUTRIENT-UPTAKES IN RELATION TO NUTRIENT-POOR SOILS

Whilst it is clear that there may be appreciable variation in the nutrient-uptakes by particular species, it is also clear from the numerous studies representing many species, growth-rates and soil types, summarized in Table IX, that no species producing timber has ever been known to make negligible nutrient-demands upon the site, and, moreover, uptakes by well growing forest appreciably lower than the Lower Fiducial Limits shown are rare.

If the reasonable assumption is made that forest growth and timber-removal of any species upon any site necessitates a nutrient-uptake and removal of the same general order and not greatly lower than the values shown in Table VIII considerable progress can be made towards a better understanding of tree growth behaviour, the silvicultural principles necessary for continued timber production upon nutrient-poor soils, and those aspects of the soil-forest relationship requiring much greater attention than they have hitherto received.

(i) *Observed phenomena*

There are two opposing schools of thought regarding the effects of coniferous afforestation in Britain. The first argues that the almost "self-perpetuating" ability of the Scandinavian coniferous forest portends well for coniferous growth in Britain, whereas the second that the numerous demonstrations in Central Europe and elsewhere of declining timber productivity consequent upon replacement of hardwood forest by coniferous and ericaceous species are bad omens.

If the idea of nutrient-removal via timber-removal is accepted the explanation of the differing forest behaviours may lie partly in the different rates at which timber, and hence nutrients, are removed from the two forest sites, and partly in the different abilities of the soils, through geological differences, to replenish, within the tree rooting zones, the nutrients, removed.

Thus, the "self-perpetuating" slowly growing Scandinavian coniferous forest, frequently upon morainic material rich in unweathered minerals, was up to the advent of the sawmill 100 years

ago, only lightly exploited, the then vigorous self-regenerations occurring subsequent to repeated natural burnings of the *entire standing forest* [68]). "Self-perpetuation" was maintained, therefore, in a forest subject to a negligibly small timber-removal and hence nutrient-removal, from the site, and although "self-perpetuation" has continued during the past 100 years of increased exploitation, this period may be too short for the increased nutrient-removal to have seriously affected soil-nutrient status and site-productivity.

The degenerated hardwood forests, on the other hand, are frequently upon highly siliceous sedimentary strata containing few minerals; the hardwood timber, often perhaps a high-nutrient containing oak, is removed and often a succession of quickly and densely grown coniferous crops, each containing appreciable quantities of nutrients, taken from the site [31]).

Clearly, if in Britain, sustained timber production upon nutrient-poor soils be the intention, and not the repeated burning of the entire standing crop, then the second example is the more analogous and declining site productivity, therefore, is a very probable danger.

But it is also important to recognize that the concept of soil degradation resulting from nutrient-removal via timber-removal must not be confined to coniferous species. P. E. Müller [38]) [39]) showed quite clearly, but perhaps did not sufficiently stress, that mor-formation upon nutrient-poor Danish soils, resulting from the introduction of beech and invasion of ericaceous species, was always taking place in oak forest which had, for a long time, been subjected to timber exploitation.

Compared with a virgin oak forest, therefore, there would have been a continuous nutrient-removal, particularly of calcium, from these sites, and it is reasonable to suspect that some decrease in absolute nutrient-content in the soil rooting zone, unfortunately undetectable by the methods of analysis then available to C. F. A. Tuxen [39]) occurred prior to the stage at which the ericaceous species invaded and continued, probably in a different way, the process of site degradation.

The persistent inability, since this time, to recognize this nutrient-removal associated with timber producing forest composed of any species, has caused one of the most important factors initiating the change from mull to mor to be repeatedly ignored, and because of this, and the valid observation that a few years' growth of certain

hardwoods can sometimes bring about decreased acidity in the surface soil horizons [48]), has encouraged many to accept, as an established fact, the fallacy that a highly productive timber forest upon a mull soil type can be produced from a relatively unproductive mor, solely by changing the floristic composition of the forest.

What, in fact, happens after many years growth of several coniferous and hardwood species upon a typical nutrient-poor *Calluna* soil is examplified below and in Diagram 2 by a comparison of pine, birch and ling on almost the same soil.

Soil characteristic (all nutrient concentrations as mg element per g soil)	Raw humus		
	P. silvestris	*Betula* sp.	*Calluna*
pH (1 : 5 H_2O)	2.9	3.2	3.1
total Ca	2.5	3.3	0.5
avail. Ca	0.50	1.65	0.20
% availability of Ca	20.	50.	41.
total N	13.3	16.4	8.2
avail. K	0.13	0.11	0.11
total P	0.46	0.64	0.39
avail. P	0.13	0.16	0.11
% availability of P	29.	26.	29.

avail. Ca & K = exchangeable; avail. P = soluble in 8-hydroxyquinoline in acetic acid.

Thus, if observations are restricted to the raw humus, and nutrient changes are looked at in the conventional way, it may be claimed that the growth of birch has an "improving", but pine, in some ways, a "degrading" effect.

But this is only part of the story, the more significant effects being illustrated in Diagram 2 by expressing the nutrients as absolute-contents.

Thus, the growth of both pine and birch not only increases the depth of the existing raw humus, but builds up upon it weights of extremely acid litter far greater than those already existing under the *Calluna*. Within these two very acid litters, considerably greater absolute weights of all nutrients, and particularly within these two raw humus horizons, very considerably greater absolute weights of non-available Ca, total N, and to a less extent non-available P, are immobilized, compared with under *Calluna*, so that the contrast in absolute nutrient content between the raw

humus and the lower horizons of the profile is being increased; because also physical investigations [56]) have shown that no structural improvement in the mineral soil horizons results from the growth of the hardwoods, it can only be concluded that upon these nutrient-poor soils the continued growth of several coniferous and hardwood species (pine, larch, beech, oak and birch) intensifies the existing mor-condition, in a manner reminiscent to that seen under the more acid permanent grass plots at Rothamsted [59]).

But apart from these nutrient-changes, others of far greater long term importance are simultaneously taking place. Thus, accepting the most conservative estimates of nutrient-uptake by the two species, which recent studies [83]) and Table XI suggest may be underestimated in the case of birch, it is seen that within these comparatively short growth periods the quantities of Ca, K and P removed from the soil and in part removed from the site are already far larger than the available quantities of corresponding nutrients in either the rooting zone or the top 50 cm soil, and particularly large is the amount of Ca taken up relative to the reserve Ca in the soil.

The inability of soils of this type to supply the nutrients taken up by timber producing forest is illustrated strikingly by the following comparison of estimates for 100 year rotations (from Table VIII) with the nutrients contained in a typical *Calluna* moor soil (from Diag. 2):

Species	Nutrient-uptakes for one 100 yr. rotation, kg per acre					
	Ca		K		P	
Pines	203		91		21	
Other conifers	438		234		41	
Hardwoods	879		225		50	
Litter	30		10		10	
Soil horizon	Nutrients contained in a Calluna moor soil, kg per acre					
	total	avail.	total	avail.	total	avail.
Top 28 cm	237	27	n.d.	17	149	19
Top 50 cm	562	36	n.d.	32	406	23

n.d. = not determined

A fundamental difference exists between these *Calluna* soils and normal forest soils (*e.g.* Thornton-dale, Diag. 2); the 100 year uptakes, except perhaps those for K, are all less, sometimes considerably, than the available nutrients within the top 50 cm of the forest soil, but for *Calluna* moor soils, the same uptakes,

particularly those for Ca and K, greatly exceed the available nutrients of the top 50 cm, this difference being further accentuated in practice because forest soils usually contain moderate concentrations of available nutrients below 50 cm exploitable by the root-system whereas moor soil horizons below 30 cm are almost devoid of available nutrients and contain less than 15% of the whole root system [56]).

Therefore, whereas upon normal forest soils, these uptakes can usually be met from the amounts of available nutrients already present, upon *Calluna* moor soils — and, in fact, upon all soils where although the available nutrients may greatly exceed those reported here, they are still less than the uptakes — the growth of all tree species necessitates release of nutrients from reserve sources, at comparatively rapid rates.

It would be difficult to prove that such rates are unattainable, but the evidence suggests them to be most unlikely upon nutrient-poor soils anywhere, partly because of the nature of their parent materials.

Here they are highly siliceous sedimentary strata which have always been poor in useful minerals; the minerals now remaining after 2,000 years of acid leaching with an annual potential percolation rate of over 500 mm, could hardly be anything but most resistant to further nutrient-release. Elsewhere they are acidic primary rocks, which as older land-forms and under higher temperatures have already weathered to most infertile residues, or which as more recent land-forms under temperate conditions, weather only slowly.

Upon soils derived from these parent materials decreases in the replenishment rates of available nutrients may be expected, therefore, when the comparatively large nutrient -withdrawals of timber producing forest are imposed upon the sites, but because the nutrient-availability and -replenishment-rates are greater within organic compared with inorganic soil constituents, a sudden rather than gradual regression in tree growth due to nutrient-deficiency may be expected upon soils with raw humus horizons, occurring firstly for "hardwoods", subsequently for "other conifers" and lastly for "pines".

An inherent difficulty associated with the use of such soils as forest land, therefore, is that although early tree growth may appear

very promising, rates of nutrient release adequate to meet the demands of timber producing forest, cannot be maintained.

Moreover, the data show a further fundamental difference between *Calluna* soils and normal forest soils; the above 100-year nutrient-uptakes are all very considerably less than the quantities of total nutrients within the top 50 cm of the normal forest soil, but for *Calluna* moor soils, the same uptakes are either large compared with the total nutrients in the top 50 cm, or greatly exceed them.

Therefore, whereas upon normal forest soils, these uptakes can usually be met from the available soil nutrients already present, upon *Calluna* soils even if nutrient-release from reserve sources could be accelerated to keep pace with the withdrawals, the supplies of at least some important nutrients *e.g.* Ca, are not sufficient for more than two rotations of any species.

In practice, however, such acceleration would not be possible, so that the sudden regression in tree growth expected from the decrease in the nutrient-release rate, could now be expected to be more acute because so negligibly small would the nutrient-release rate become that the sole nutrient-movement possible (as discussed in an earlier section) would be that associated with foliar flush and fall, there being negligible nutrient-uptake for immobilization in woody tissue, or in other words, negligible timber production.

A further difficulty associated with the use of such soils as forest land, therefore, is that at least some of the important nutrients required for continuous timber production are just not present in the soil in sufficient quantity.

It is clear, therefore, that although early tree growth upon such soils may appear very promising the continued exploitation of these soils for timber production by the methods widely used today can only cause further site impoverishment and, eventually, the destruction of the timber forest itself.

It is of some considerable practical importance to enquire, therefore, whether the forester would be best advised to resort to species — the pines — producing the greatest volume of timber for the least uptake of nutrients before being forced to abandon the sites, or whether any other methods exist whereby the sites might be maintained under timber producing forest.

It has sometimes been claimed that the growth of certain "soil improving" hardwoods, either pure or in mixture with conifers,

can either convert such soils into highly timber productive brown-forest soils, or restore the brown-forest soil that possibly existed on such sites before Bronze Age times [17] [18].

Such claims, however, fail to recognize that ordinary leaching [15] and podzolisation [12] [60] processes, operating over the past 2,000 years, have not immobilized in non-available form certain important nutrients *within* the site, but have caused such large quantities of these nutrients to be *removed from* the site altogether, that the present soils differ fundamentally from their former condition in simply not containing the nutrients necessary to support continuous forest growth, quite apart from those required to re-establish a brown-earth.

Thus, although the failure of some 60 years' growth of birch, oak, holly and beech to bring about this conversion has been demonstrated in practice and examined above, some consideration of the soil changes a "soil-improving" species would have to bring about, and its own demands upon the soil, explain why this conversion is an impossibility.

Thus, the top 50 cm of a most degraded or nutrient-poor brown-earth (Scampston, Diag. 2) contains 1496 kg total Ca and 676 kg available Ca per acre, and the top 100 cm, 3146 kg total Ca and 1232 kg available Ca: the top 50 cm of a typical *Calluna* moor soil contains 562 kg total Ca and 36 kg available Ca, and the top 100 cm 1302 kg total Ca and 56 kg available Ca.

The overall Ca-uptake of one 100-year rotation of a "soil improving" hardwood depends upon species and growth-rate, but probably lies between 200 and 600 kg Ca per acre (Table IX).

Hence, however efficient were the hardwood in converting 'total' into 'available' Ca and in bringing Ca from the lower to the upper horizons within the top 100 cm of the *Calluna* soil, there is just not sufficient total Ca present in these horizons both to produce the Ca-status of the brown-earth and provide the Ca-uptake of the tree crop, quite apart from the Ca-requirements of the other forms of life within the mull habitat, whilst the data of Diag. 2 show a similar difficulty in respect of P.

The evidence suggests, therefore, that many of the nutrient-poor soils being afforested today differ fundamentally from forest soils in one of two ways. Either

(i) the nutrients required for continuous timber production are simply not present in the soil, or

(ii) if present in reserve form, may be released in available form at rates inadequate to meet both the growth demands of the forest and the unavoidable leaching losses from the site.

Upon the first type of nutrient-poor soil, therefore, the maintenance of continuous timber production and soil changes away from extreme mor-conditions are not primarily questions of rendering reserve nutrients available *within* the site, but of introducing available nutrients from *extraneous* sources, upon the second type of nutrient-poor soil, although direct root activity of certain tree species upon reserve soil minerals [6]) may enable the nutritional requirements of a tree crop to be met, it may be that in practice, as before, the introduction of available nutrients from extraneous sources may be necessary to obtain economic timber production.

(ii) *Silvicultural principles for sustained timber production*

It is now possible to suggest broadly the cultural operations necessary to ensure continuous timber production upon nutrient-poor soils.

Firstly, all adverse factors, such as water-logging, able to restrict the full root-exploitation of all soil horizons and hence nutrients, should, as far as is practicable, be removed by conventional ploughing or draining operations, but it is important to recognize that ploughing cannot otherwise increase the nutrient-reserves of the site.

Secondly, very considerable reductions in the nutrient-removal from the site, can be achieved, during timber extraction, without detriment to stemwood production by leaving the brush and stembark on the forest floor.

Thirdly, the nutrients lost from the site via the timber must be replaced by the use of soil-ameliorants. Nutrient-poor *Calluna* moor soils very similar to the Silpho site in Diag. 2 have been converted into mull soil-types, (the Ebberston site, Diag. 2), able to support superior tree growth, and species normally failing upon the unreclaimed moor, whilst numerous examples [5]) [23]) [33]) [44]) show that superior growth is obtainable simply by applying ameliorants. Experimental work has shown that not all attempts to increase growth-response by this method are successful [72]) and it is com-

paratively easy to bring about undesirable fungal increase [58]) or disturbance of nutrient-balance [61]). Clearly there is much to be learned regarding the ameliorant materials and methods of application suited to particular soils and environmental conditions.

For the soils considered above, materials able to replenish Ca-losses would appear most appropriate (although it has also been shown [56]) that these soils show the rather uncommon property of being at once very acid and of very low manganese status [9]) [14])) but for other sites, detailed studies may reveal other deficiencies. More permanent growth-response is to be expected from the coarsely ground basic minerals as used by N e m e c in Central Europe [44]) and by the writer in this country, rather than by ameliorants designed for the quicker growing agricultural crops. An idea worthy of trial, however, is the combination of the more permanent ameliorant with those already known, *e.g.* basic slag, to give a marked stimulus over the first 15 years' growth.

It is important not to imagine, however, that the raising of the soil-nutrient-status by an ameliorant is all that is required for the fullest productivity of the site; for to achieve the latter it may well be that certain associates of the more fertile forest community, for example, shade tolerant shrubs, are necessary to provide palatable food to mull-forming fauna [42]) and yet which by their high foliar: woody organ growth development ratio do not exercise a serious nutrient-demand upon the site.

For certain conditions it has been argued — possibly, quite rightly — that ameliorants cannot be afforded, but to the forester upon nutrient-poor soils, anywhere, the important question is not whether the cost of the ameliorant will be recoverable by increased timber-production, but whether for lack of a relatively small extra expenditure the survival of forest and the orginal heavy establishment costs are to be sacrificed.

(iii) *Aspects of the soil-forest complex requiring further attention*

It may now be seen that a consideration of the nutrient-removal by timber-producing forest in relation to the nutrient-supplying ability of the site is a concept of considerable practical importance.

This concept has been developed for certain nutrient-poor British soils, as far as existing data permit, but its full practical value, both here and elsewhere, cannot, at the moment, be realized

because of the many fundamental studies, needed to provide the necessary data, still requiring to be undertaken.

Thus, three studies [4] [40] [67] and the above data represent almost our total knowledge of the relative proportions of available and reserve nutrients within a soil, whilst the replenishment of the former from the latter, under natural conditions, does not appear to have been investigated; similarly no nutrient-uptake studies have ever been carried out in Britain upon the common forest species.

As in this country, the difficulties of forest-establishment have been largely overcome, methods necessary to maintain and perhaps improve site-productivity by the use of ameliorants now merit serious attention.

Extensive experimentation in Continental Europe [3] [8] [11] [32] can provide a selection of the more promising materials and methods, but long term experimentation needs considerable extension now, if conclusions concerning growth-response and soil changes are to be available before such methods become a widespread silvicultural necessity.

CONCLUSIONS

Nutrient composition data for a wide range of individual mature temperate forest trees of different growth rates and from varying soil types are able to give reasonably valid mean estimates for the nutrient uptakes of mature hardwood and coniferous forest growth on an area basis, but are too limited to yield precise estimates for particular species upon particular sites.

The quantities of all three nutrients calcium, potassium and phosphorus taken up decrease in the order: "hardwood", "other conifer" and "pine", forest. All three types of forest take up considerably less potassium and phosphorus compared with agricultural crops, but the amounts of calcium are not greatly less; moreover, as all except very young forest growth differs from agriculture in taking up calcium, and not potassium, in greatest amount, the importance of calcium to forest growth appears to have been hitherto markedly underestimated.

From the distribution of the nutrients among the various tree organs is deduced a most important fundamental difference between

timber-producing and unexploited virgin forest not apparently recognized hitherto. Within a comparatively short time from the establishment of timber producing forest composed of any species, the overall-nutrient demand (by the forest) on the site is made up in greater amount and subsequently in ever increasing proportion by a nutrient-removal from the site via timber thinnings rather than a nutrient-immobilization in the tree organs of the growing forest within the site; hence, the longer timber exploitation is continued the more does nutrient-removal from the site, especially of calcium, become an increasingly important long term effect of forest growth upon the soil. Within virgin and stagnated forest, however, this continuing nutrient-demand is absent.

To the forester interested in continuous timber production, therefore, the vital issue is whether his soil possesses the ability to replenish continuously the nutrients being removed via the timber, but the "self-perpetuation" or even existence, of a virgin forest upon a similar soil, or even formerly upon the same site, is quite irrelevant.

Upon nutrient-rich soils this nutrient-removal may be of little silvicultural significance, but upon many nutrient-poor soils, some of which have been accepted as potential timber-producing land, it is believed that the persistent inability to recognize this nutrient-removal by all timber species, has caused one of the most important primary factors imitiating soil degradation and diminishing site productivity to remain undetected, and, in consequence, has engendered the fallacy that these important site characteristics can be changed at will solely through the floristic composition of the forest.

Data representative of many nutrient-poor Yorkshire (England) *Calluna* soils show that nutrient-uptake estimates for both pine and birch timber-producing forest in relation to the available and reserve absolute nutrient-contents of their sites not only far exceed the relative nutrient-demands of an agricultural crop to an agricultural soil, but also that, certainly for calcium, both the quantities of nutrients required for continuous cropping of either species and the quantities which birch has been accredited in being able to make available in the upper soil horizons are simply not present in the soil profile, even in reserve form.

Furthermore, as it is shown that for all three types of forest the

ratio of the nutrients returned to the soil via the foliage to the nutrients immobilized within the woody organs is similar, it seems improbable that any particular species can have an exceptionally favourable effect upon the nutrient-status of the surface soil horizons without simultaneously making correspondingly larger nutrient-demands upon the other horizons, and hence ultimately a greater absolute overall nutrient-removal, unless the species is either allowed to rot upon the site or is characterized, as in the case of shrubs, by a high foliar:woody organ growth-development ratio.

The forester upon nutrient-poor soils, therefore, must recognize not only that further soil degradation and seriously reduced productivity must inevitably follow conventional silviculture, simply because the sites themselves cannot support this form of utilization, but also, that palliatives such as reploughing, conservation of nutrients by removal of stemwood only, resort to less nutrient demanding species, and growth or admixture of hardwoods, all fail to create sound husbandry because none puts back into the site the nutrients required to maintain productivity.

For a variety of Yorkshire *Calluna* soils, and almost certainly for many nutrient-poor soils throughout the world, continuous timber production is not possible until rather special silvicultural techniques are developed which, as in non-primitive agriculture, primarily base the maintenance of site productivity on the use of soil-ameliorants.

At the moment, the forester in this country, and elsewhere, cannot prescribe these techniques, because he knows almost nothing of the nutrient-removals by his crops, the nutrient-supplying ability of his soils, and the ameliorative materials and techniques suitable for particular sites.

Considerable intensification of fundamental and experimental research upon these complex aspects is necessary, therefore, if in forestry, as in agriculture, production is to have a scientific and not speculative basis.

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THE EFFECT OF LIGHT UPON THE ROOTS OF BEECH AND ITS SURFACE POPULATION

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INTRODUCTION

The growth of plants in different intensities of daylight leads to changes of their internal processes and alterations of their relationships with the microflora associated with their root systems. There is no conclusive evidence that the effects on the associated microflora are influenced by any single factor operating in the tissues of the host plant and in all probability there is a whole series of factors and interactions in operation.

The influence of light intensity upon the susceptibility of plants to pathogens is illustrated by the work of Eaton and Rigler [4]) upon the resistance to *Phymatotrichum* root rot of cotton plants. The seedlings were unsusceptible to the rot but the resistance of older plants was dependent upon the carbohydrate content of the root bark. In one experiment, the carbohydrate content of the roots was adjusted by leaf and flower mutilation and it was shown that a low carbohydrate content favoured the growth of all types of bacteria on the roots except blue-green fluorescent forms which were more abundant on roots with the highest carbohydrate content.

The physiological condition of seedlings influences the stage and nature of plant infection. This applies also to symbionts where infection usually follows the unfurling of green leaves and the initiation of photosynthesis. Infection of lucerne seedlings by nodule forming bacteria commences at the time when the first leaf unfurls (Thornton [16])) and mycorrhizas of the ectotrophic type are formed on the

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root systems of forest trees after the appearance of primary needles in the case of certain pine species (Huberman [10]) and after the expansion of the first pair of leaves in the case of beech seedlings (Harley [7]), p. 142).

The commencement of infection in these cases may not be entirely dependent upon the carbohydrate level in roots but on the formation of other metabolic products. Thornton [16] [17]) showed that lucerne roots exude a substance which stimulates the growth of bacteria and showed that delay in infection of the seedlings was due to the condition of the host plant and was not dependent upon the infective power of the inoculum. It was suggested that the availability of carbohydrates to the bacteria might determine the balance between the host root and the associated bacteria in this type of infection since it was found that when plants were grown in the dark the nodule forming bacteria became parasitic.

Björkmann [1] [2]) has put forward the hypothesis that it is partly the quantity of carbohydrates present in the roots of forest trees that determines the occurrence and intensity of mycorrhizal development. Consequently, factors such as high intensities of daylight and low availabilities of nitrogen or phosphorus which tend to favour the maintenance of a high level of carbohydrates lead to an increase in the development of mycorrhizal roots. It is difficult, however, to evaluate the influence of soluble carbohydrates on the nature of microbiological infection since changes in the concentration of sugars can be correlated with changes in concentration of other metabolic products.

This is an account of an experiment which was made in 1953 to determine how the fungal flora of the surfaces of the root system of beech seedlings, during their first year, was affected by growth in varying intensities of daylight. The account is of a descriptive nature, in which the frequencies of various types of mycelia encountered on the sampling plates is given. There will be no attempt in this account to describe any of the internal and external factors operating within the host tissues which might influence the nature of the root surface populations. A full description and discussion of a method of sampling active mycelia on surfaces in soils will appear elsewhere (Harley and Waid [8]).

METHODS

Conditions of seedling growth

Beech seedlings were grown in frames in which the intensities of daylight were varied but under otherwise uniform environmental conditions. Four experimental frames were constructed side by side in the greenhouse. The North, top and South sides of each frame were covered in butter muslin and the East and West sides were made from Sizalkraft paper. The frames were one metre in height but the South face was at an angle of 45° to the vertical to permit the exposure to sunlight of a large area of muslin. A gap of 15 cm between the base of the frames and the greenhouse floor permitted the free ventilation of air between the frames. The gap was shielded by a low brick wall to prevent the direct penetration of sunlight into the frames. Another batch of pots containing seedlings was arranged on the floor of the experimental greenhouse.

The amount of daylight radiation was controlled by varying the number of layers of butter muslin on each frame. Measurements of light intensity were made with a Weston Mark II Universal Exposure Meter which was supported over a large sheet of white cartridge paper (2000 sq. cm) to record the intensity of reflected sunlight. The relative intensities are shown as a percentage of the daylight radiation in Table I. There is no information concerning the daily fluctuations in temperature humidity in the frames, nor upon the differences in these factors between treatments though the latter was to a certain extent controlled by free ventilation between the frames.

Pots, 24 cm high and 8 cm in diameter made of Sisalkraft paper were filled to the brim with soil which had been collected from a stand of beech in Bagley Wood, Berkshire. This has an acid soil (pH 5.5) lying above plateau gravel in which mycorrhizal roots of beech are found in abundance in the humus layer just below the layer of raw beech leaf litter. Three seeds, from a uniform sample obtained from the Forestry Commission, were buried at a depth of one centimetre in each of the pots on the 27th April, 1953. All the pots were kept on the floor of the greenhouse but were transferred to one of the experimental frames as soon as one seedling per pot germinated. Care was taken to ensure that each experimental frame was provided with plants that had germinated on similar

dates. All the viable seeds were considered to have germinated by the end of May when the soil was covered with pieces of broken earthenware to shade its surface and to prevent the growth of algae and bryophytes. Records were made of the growth of each seedling.

The pots were watered at intervals and care was taken to ensure that the soils in all the pots were equally moist. Measurements were made on several occasions of the water contents of the soils by weighing before and after drying at 70°C and little variation occurred in the five treatments.

Selection of seedlings for sampling

Samplings were carried out by selecting one pot from each of the five populations of seedlings. Care was taken to ensure that each pot contained the same number of seedlings and that at least one seedling in each pot had germinated at the same time as the seedlings representing the other treatments. The number of pots per treatment was limited to eight and where a choice of plants occurred bias was reduced by selecting the most healthy looking plant. The fungi active on the root surfaces of these five seedlings, one per treatment and all of similar age, were sampled by the method described below. The remaining plants were retained for further examination and measurements.

Examination and measurement of seedlings

The root systems of the seedlings were examined externally and were then examined under the low power of the microscope to ascertain the presence and type of ectotrophic mycorrhizal infection and to determine the presence of other kinds of root surface fungi.

Measurements were made of stem and root length and the number of leaves per plant was counted. The seedlings were then dried at 80°C for 24 hours and the dry weights of the stems, leaves and roots were recorded.

Estimations of the soluble carbohydrates in roots

The extraction of soluble carbohydrates was performed by following the procedure of Y e m m [21]) except for two minor modifications. First, the roots were given a quick wash as soon as

they were removed from the soil and before the sugars were extracted in 80% ethanol. Secondly, during the process of decolourising the extract the alcohol free residues were taken up in warm water and filtered through colloidal aluminium hydroxide but the residues were not boiled with activated charcoal.

Soluble sugars in the roots of the beech seedlings were estimated by employing the method of Somogyi[15]). The results are expressed as the glucose equivalent by weight of reducing sugars. The glucose equivalent by weight of hydrolysable sugars was obtained by hydrolysis with 10% sulphuric acid.

The method of sampling the surface fungi of the root systems of the seedlings

A method of sampling fungi which are active on the surfaces of roots has been described elsewhere by Harley and Waid[8]). The details of the procedure which was followed in this experiment are outlined in this section.

A 5.0 cm length of tap root and a total of ten 1.0 cm lengths of the lateral roots of selected seedlings were washed separately in sterile phials in 10.0 ml of sterile water. The phials were shaken on a horizontal shaking machine at the rate of 300 beats per minute. The water in the washing phials was changed every 2 minutes by decanting away the washings and adding a further 10.0 ml to the phials. This process was repeated 20 times for each of the phials.

The washed roots were cut into 0.2 cm lengths and as they were cut the fragments of root were implanted onto nutrient agar. Five fragments or 1.0 cm of root was implanted onto each plate.

The nutrient agar medium was that of Lochhead and Chase[11]) slightly modified. Cultures were incubated at 25°C in the dark for the first three days and then on the laboratory bench for a period of 12 weeks. Plates were examined on the 3rd, 7th, 13th and 84th day and on various other occasions during the incubation period.

As far as possible each fungal colony was identified or given a code number. Results of the counts of fungi are shown in the tables either as the number of occurrences per 100 fragments of root or as the percentage of plates on which it occurred.

RESULTS

Seedling growth

The beech seedlings had all developed a pair of true leaves by the beginning of July, *i.e.* 2 months from planting. Even at that early date differences in the dry weights of seedlings growing in the different intensities of light were apparent, so that those grown in the higher intensities of light were heavier than those grown in the lower (see Table I). The plants growing in deep shade increased little in dry weight throughout the summer and produced only one pair of leaves. Their stems were weak and their root systems were poorly developed so that the ratio of the dry weights of root and shoot was low. On the other hand, the plants receiving higher intensities of light were more vigorous in their growth, their shoots were woody and produced more leaves which were larger and of a deep green colour. Their main roots were woody and the lateral root systems were very well-developed so that their root and shoot ratio was higher. Similar observations have been recorded elsewhere (see Harley[5], [6] p. 141).

TABLE I

The growth of beech seedlings in frames covered with varied number of layers of muslin in order to alter the light regime between treatments. Results obtained on two sampling dates are shown as mean dry weights of whole plants, the ratio of dry weight of root to shoot and the number of leaves per plant on the second date of sampling

Layers of muslin	0	1	2	4	8
% Daylight radiation	25.1	14.2	10.6	6.1	3.6
Dry weight in mg of whole plant					
2 July	616.1	310.6	214.9	174.8	159.5
17 September	1569.4	662.5	430.7	348.3	154.1
Ratio roots/shoot					
2 July	0.449	0.247	0.337	0.126	0.163
17 September	1.060	0.629	0.586	0.260	0.155
Number of leaves, 17 September					
Leaves	7	3	3	3	2
Cotyledons	0	2	1	2	2

The results of the estimations of soluble carbohydrates (see Table II) demonstrate, as anticipated, that the total weight and the proportions of soluble sugars in the root tissues increased with increase in daylight intensity. Taken together with the results of the mycorrhizal infections described below, the results of the sugar analyses show good agreement with the experiments of Björkmann[1], [2].

TABLE II

Soluble carbohydrates extracted from the roots of beech seedlings grown in varied intensities of daylight expressed as glucose equivalent. Results are shown as the total weight of sugars and as a percentage of dry weight of root

	% Daylight radiation				
	25.1	14.2	10.6	6.1	3.6
Total weight of sugars in mg. . .	27.8	10.1	3.7	2.1	0.4
Total sugars as a percentage of dry weight of root.	3.5	3.9	2.3	2.9	1.9

Root infection

Various kinds of mycorrhizal and parasitic infections developed on the lateral root systems between mid-July and the end of August, that is, just after the first pair of true leaves had developed. The type of infection varied from treatment to treatment and although no counts were made of the numbers of infected roots of each morphological type their relative frequencies were estimated by eye and these are shown in Table III.

TABLE III

Different types of root infection observed on the root systems of beech seedlings grown in varied intensities of daylight. The degree of infection is expressed by a subjective method *)

Mycelium colour	% Daylight				
	25.1	14.2	10.6	6.1	3.8
Infection of the mycorrhizal type					
White	++	+	—	—	—
Brown	+++	+	—	—	—
Black	++	++	++	+	+
Parasitic lesions					
Black	—	—	—	+	++

*) +++ abundant infection. + present.
++ frequent. — absent.

Mycorrhizal infections. The most abundant type of mycorrhizas were light-brown in colour and the infected lateral systems consisted of many short branches orientated at right angles to the main axis. Mycorrhizas with white mantles were less frequent but the morphology of the infected lateral systems was similar to those with a light-brown mantle. These two types of infection which were associated with the presence of branching strands of hyphae were observed on seedlings growing in the two highest levels of light intensity. The light-brown mycorrhizas are similar

to the types of mycorrhiza which are found in abundance on beech in the humus layers of the woodland from which the soil was removed for this experiment. In culture, sterile fungi with brown hyphae developed from infected lateral roots of the seedlings but their growth was very slow and they were invariably overgrown by more rapidly growing forms.

Another type of mycorrhizal infection was observed on solitary laterals. A black fungal mantle developed which was beset with straight unbranched hyphae arising in great numbers at right angles to the surface of the mantle. This type of infection was observed on all seedlings growing in light intensities greater than 10.6% daylight and occurred less frequently on plants grown in deep shade. This type of infection resembles that due to the jet black mycelium described by Hatch [9] and known as *Mycelium radicis nigrostrigosum* or *Cenococcum graniforme*. This fungus has been isolated by Harley from roots of beech and from mycorrhizas of a similar type described by Wilson [20].

These results are in good agreement with the reports of Björkmann [1] [2] who found that in Sweden mycorrhizas of varying appearance were differentially developed on the root systems of pine and spruce in different intensities of daylight. Björkmann [1] considered that the types of mycorrhiza which can be found in abundance on naturally infected roots of pine and spruce are the most important and these were called Mycorrhiza A & B. The quantity of A & B mycorrhizas increased greatly between 12 and 23% daylight on roots of pine and between 6 and 23% daylight on roots of spruce.

The results presented in Table III demonstrate that the types of mycorrhiza which are most abundant on adult beech in woodlands are most abundant on beech seedlings growing in 25% daylight, less so on those growing in 14% and absent from plants grown in 10.6% daylight.

Mikola [13] reported from Finland that *Cenococcum graniforme* could form a mycorrhizal association with birch at light intensities as low as 10% and Björkmann [2] has found that the same species forms mycorrhiza with pine at 12% daylight radiation. Table III shows that the black mycelium formed mycorrhiza with beech in intensities of light at 10.6% and was occasionally found on seedlings in the lower intensities.

Parasitic infection. Another type of infection was seen on the roots of beech seedlings which were grown in deep shade and this consisted of dark brown to black parasitic lesions which were not associated with radiating hyphae. These were first seen on the lateral roots of plants growing in the lowest intensity of daylight (3.6% daylight) on the 17th July. From these lesions mycelia resembling *Rhizoctonia sylvestris* and the *Mycelium radicis atrovirens* type were isolated on the sampling plates (Melin [12]). This result is of interest since Vaartiga [18] has reported from Finland that the rate at which "damping off" of seedlings occurs in seedling beds is increased when the seed beds are shaded. His results showed that many of the fungal isolates were enabled to become parasitic

TABLE IV

The surface fungi of the tap roots of beech seedlings grown in different light intensities. The frequencies are shown as the number of times each fungus occurred on 100 2-mm portions of root after washed portions had been incubated on nutrient agar plates for 12 weeks (100 portions of root were sampled)

	% Daylight radiation				
	25.1	14.2	10.6	6.1	3.6
Segments free of fungi	11	6	5	3	1
Trichoderma	**72**	43	45	22	36
Gliomastix	**21**	17	12	7	12
Sterile hyaline	**8**	2	1	6	3
Brown sterile	4	**15**	14	6	4
Hyalopus	0	**6**	1	1	3
Oospora	0	**5**	3	2	2
Calcariosporium	26	11	**33**	17	15
Gliocladium	7	6	**10**	5	6
Ophiostoma	0	0	**8**	2	2
Cylindrocarpon	25	31	51	**59**	44
Penicillium	1	4	8	**8**	8
Paecilomyces	4	6	10	**13**	4
Dark sterile	0	0	0	**8**	1
Monilia	3	2	6	**6**	5
Rhizoctonia	1	19	22	**32**	23
"Chlamydospores"	1	0	4	**7**	7
Verticillium	4	8	5	5	8
Penicillium B	39	34	49	43	**58**
Mortierella	3	6	9	7	**12**
Mucor ramannianus	1	3	3	1	**7**
Ascomycete	1	1	1	2	**8**
Various	3	10	1	3	4
Total	224	229	296	262	272

under conditions of low intensity of daylight, which indicates that a change in the resistance of the seedlings had occurred.

The composition of the root surface populations

The composition of the populations of fungi developing from fragments of root varied from treatment to treatment and also changed as the season advanced so that it is very difficult to describe the changes in tabular form. Tables IV and V record the frequencies (as number of occurrences per 100 segments of root) of the majority of the different kinds of fungi observed on fragments of tap and lateral root. These frequencies differ because the numbers of fungi on portions of lateral roots were fewer than on tap roots. The presence of fewer fungi on laterals can be ascribed partly to the fact that the portions of lateral roots had a smaller surface area than the tap roots.

TABLE V

The surface fungi of the lateral roots of beech seedlings grown in different light intensities. The frequencies are expressed as the number of records of each fungus per 100 2-mm portions of lateral root after washed portions of root had been incubated on nutrient agar plates for 12 weeks. 150 portions sampled.

	% Daylight radiation				
	25.1	14.2	10.6	6.1	3.6
Segments free of fungi	24	21	18	13	18
Trichoderma	**22**	7	8	13	5
Gliomastix	**15**	13	1	3	5
Brown sterile	5	**11**	1	3	5
Cylindrocarpon	5	**23**	22	19	18
Penicillium B	3	**16**	11	6	2
Dark hyphae	5	5	**13**	4	11
Monilia	7	3	6	6	0
Calcariosporium	1	3	5	**11**	5
Penicillium	3	5	4	5	1
"Chlamydospores"	14	2	9	**17**	11
Verticillium	3	3	0	**5**	1
Clathrosphaerina	0	0	0	1	**5**
Sterile hyaline	6	4	6	9	**18**
Rhizoctonia	5	19	26	34	**38**
Mortierella	3	5	3	2	**8**
Various	9	10	15	6	4
Total	106	129	130	144	137

In general the distribution of different kinds of fungi on the surfaces of tap and laterals were very similar. For example, *Gliomastix convoluta* and species of *Mortierella* were most abundant on the roots

of plants grown in the highest and lowest intensities of light respectively. The results indicate quite clearly that the environmental conditions of the various treatments in some way influenced the surface fungi and led to the differentiation of several distinct populations. There is little information concerning the ecology of the various isolates to warrant a fuller discussion of their frequencies on the plants receiving various treatments. However, the distribution of two of the commoner forms deserves more detailed discussion.

TABLE VI

Distribution of *Rhizoctonia* on the surfaces of tap and lateral roots of beech seedlings grown in varying intensities of daylight. Counts of *Rhizoctonia* on 25 fragments of tap root and 50 fragments of lateral roots are shown for various dates of sampling

Days from planting	% Daylight radiation					Total
	25.1	14.2	10.6	6.1	3.8	
Tap roots						
30	0	8	1	1	2	12
66	1	1	6	10	13	31
81	0	9	15	11	4	39
126	0	1	0	10	4	15
Total	1	19	22	32	23	
Lateral roots						
30	7	0	3	2	6	18
66	0	21	5	22	40	88
126	0	7	31	27	10	75
Total	7	28	39	41	56	

The distribution of *Rhizoctonia* and *Trichoderma viride*. *Rhizoctonia* was more abundant on the root surfaces, especially the surfaces of lateral roots, of plants which were grown in deep shade where it appeared to be associated with the black lesions seen on the roots of the shaded plants (Tables III, IV and V). The records of the frequency of this fungus on the main and lateral root systems at various sampling dates are shown in Table VI. In July, *Rhizoctonia* was very abundant on the roots of the shaded plants but by September its numbers had decreased. It seemed possible that the decrease might have been influenced by two factors operating either separately or in conjunction. These two factors are first the condition of the host plant and second the

influence of organisms antagonistic to the growth of *Rhizoctonia*.

Trichoderma viride is well-known as soil fungus which can overgrow or inhibit the growth of many other fungi in culture. There are several reports that this fungus can antagonize root-infecting fungi under certain soil conditions (Rishbeth[14]; Bliss[3]). Weindling[19]) was the first to report that it parasitised *Rhizoctonia* in acid soils.

TABLE VII

Distribution of *Trichoderma viride* on the surfaces of tap and lateral roots of beech seedlings grown in varying intensities of daylight. Counts of *Trichoderma viride* on 25 fragments of tap root and 50 fragments of lateral roots are shown for various dates of sampling

Days from planting	% Daylight radiation					Total
	25.1	14.2	10.6	6.1	3.8	
Tap roots						
30	1	1	0	0	0	2
66	22	11	11	11	9	64
81	24	11	17	2	9	63
126	25	20	17	9	18	89
Total	72	43	45	22	36	
Lateral roots						
30	0	0	1	1	0	2
66	18	6	8	11	1	44
126	15	5	3	8	7	38
Total	33	11	12	20	8	

The rate at which *Trichoderma viride* colonised the surfaces of tap and lateral roots grown in different light intensities is shown in Table VII and it is apparent that its colonization was favoured on those plants grown in the higher intensities of light.

The numbers of *Rhizoctonia* and *T. viride* on root surfaces as estimated by the sampling method appear to be inversely related (see Fig. 1). It is therefore necessary to inquire whether *T. viride* actually antagonised *Rhizoctonia* upon the root surfaces especially as it undoubtedly overgrew and antagonised it on the sampling plates making *Rhizoctonia* often difficult to detect. An analysis of the relative frequencies of these two fungi as they occur together on sampling plates is shown in Table VIII. Each plate had been

inoculated with five fragments of root and could therefore bear a maximum number of 5 specimens of any single fungal species. The data shows that the number of *Rhizoctonia* per plate was inversely correlated with the numbers of *T. viride* and that it was

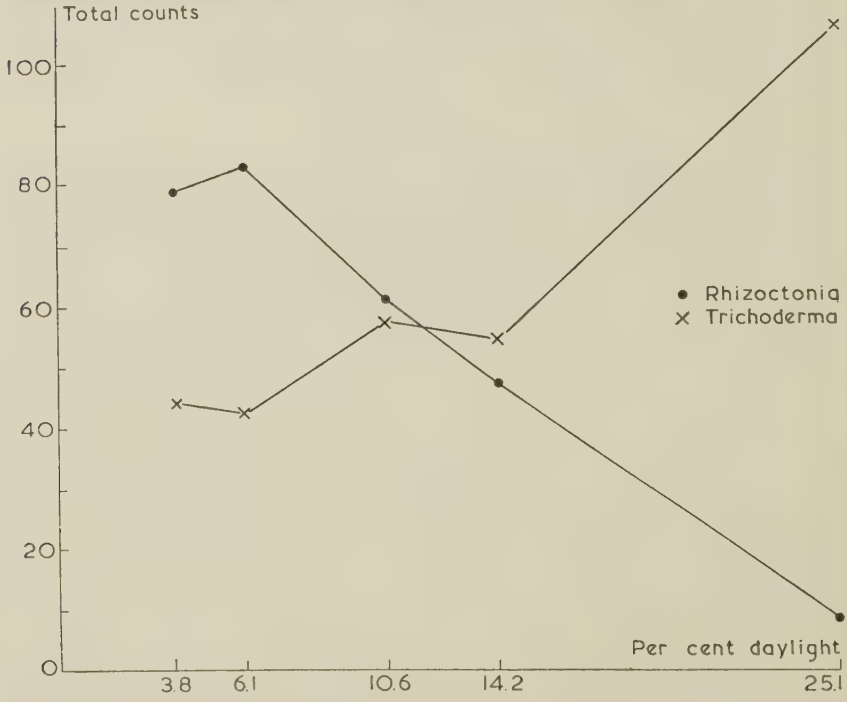

Fig. 1. The effect of varying light intensities upon the numbers of *Rhizoctonia* and *Trichoderma*.

TABLE VIII

Distribution of *Trichoderma viride* and *Rhizoctonia* upon sampling plates. The mean number of colonies of *Trichoderma* are shown on plates bearing different number of colonies of *Rhizoctonia*. Each plate was inoculated with five fragments of root and could therefore bear up to 5 specimens of any one species

Number of colonies of *Rhizoctonia*. . .	0	1	2	3	4	5
Mean number of colonies of *Trichoderma viride*.	2.63	0.94	1.19	0.77	0.36	0.06

possible that the changes of frequency of *Rhizoctonia* were secondary to those of *Trichoderma*. Fig. 1 then, might misrepresent the frequency of Rhizoctonia on the root surfaces owing to the occurrence of large numbers of *Trichoderma viride*. *T. viride* grows very rapidly

in culture and it may be assumed that its frequency was fairly estimated by this sampling method. It is necessary then to determine how far its presence led to an underestimation of the

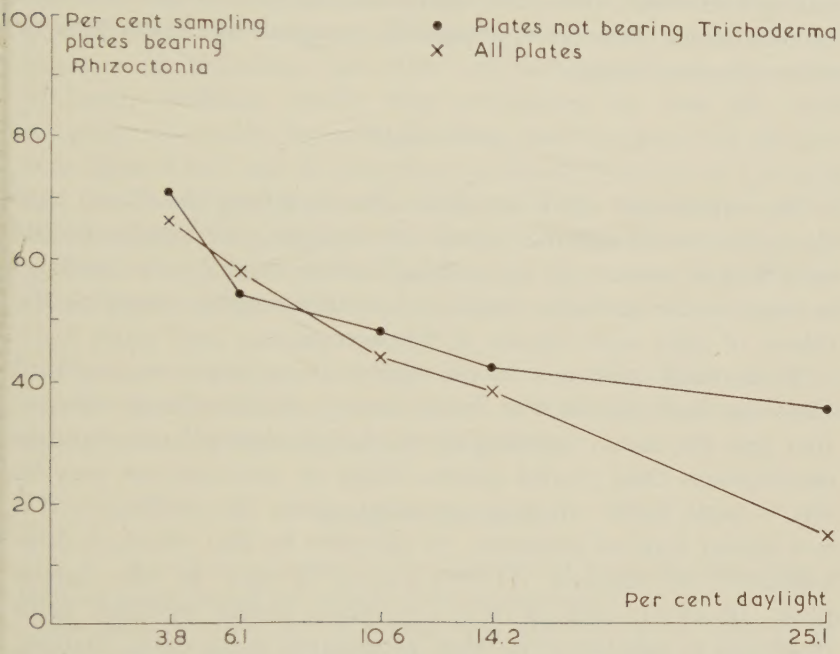

Fig. 2. The effect of *Trichoderma* upon the proportion of plates bearing *Rhizoctonia*.

frequencies of *Rhizoctonia*. To do this the presence or absence of the two fungi on each sampling plate has been considered separately and the percentage of plates which did not bear *T. viride* but bear *Rhizoctonia* has been estimated. These results are shown graphically (Fig. 2) and it can be seen that *Rhizoctonia* was present on approximately equal proportions of plates whether the *Trichoderma* was present or not.

It seems then, that *T. viride* had only a slight influence on the growth of *Rhizoctonia* in the various treatments. It is not possible to ascertain from the data whether antagonism had actually occurred on the root surface before the time they were sampled. The only conclusion that is permissable is that it was the condition of the beech seedlings which finally determined the nature of the

root surface populations. It is not possible, however, to explain the decline in numbers of *Rhizoctonia* in September. It is also possible that *T. viride* had either antagonised *Rhizoctonia* or alternatively during a secondary phase of fungal succession had occupied portions of root which had been previously occupied by *Rhizoctonia* or other species of fungi.

DISCUSSION

The experiment which has been described here has shown that the influence of different levels of daylight radiation upon the growth and nature of mycorrhizal infection of beech seedlings is very similar to those obtained by other workers studying the effects of light upon species of forest trees.

Mycorrhizal infections on the root systems were not seen until after the first pair of true leaves were unfurled though even at that time the plants receiving the most light showed more vigorous development than shaded plants. Delay in root infection may be due to some factor which is operating within the seedlings and it is a similar form of resistance to infection to that which is demonstrated by legumes (Thornton[16]) and by the cotton plant (Eaton and Rigler[4]) where young seedlings show resistance to infection even when germinated in the dark. Shading, however, eventually led to a loss of resistance by the beech seedlings to parasitic infection whilst increases in light intensity resulted in mycorrhizal formation. The differential effect of the various treatments is reflected in the quality of the visible infections and the composition of the root surface populations. It is apparent from these results that the condition of the host plant is a major factor in determining the nature of the surface population of the root system, but it is not certain how far interaction between microfungi influences the composition of this population.

The survey of root surface forms suggests that the growth of several crops of seedlings in sub-optimal conditions is a possible factor producing the degradation of forest tree nursery soils since it was found that the shading of seedlings resulted in an increase in the numbers of semipathogens in the populations on the root surfaces. The accumulation of these organisms in these soils would lower the chances of seedling survival.

It is interesting in this connection that the results of another series of pot experiments have shown that soil conditions and the nature of the initial infection of seedlings may have a profound effect on the subsequent growth of beech trees. It was found that a soil from a forest nursery at Kennington (Berks) contained large numbers of *Rhizoctonia* and other soil borne pathogens. The roots of beech seedlings, which were germinated in this soil, were naturally infected by these fungi and the seedlings were less vigorous than those which had developed mycorrhizas at the age of 6 months and had been grown in soils obtained from two mature beech stands. After one year's growth in pots the seedlings were transplanted to a garden soil and at the age of two and a half years those plants germinated in woodland soils were more vigorous than those from nursery soil.

The two experiments when viewed together show that the conditions of seedling growth have a lasting influence on the subsequent development of the organism.

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